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Hybridization as a stimulus for adaptation to a novel environment

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I am submitting herewith a dissertation written by Dylan Robert Dittrich-Reed entitled "Hybridization as a stimulus for adaptation to a novel environment." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

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Hybridization as a stimulus for adaptation to a novel environment

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This dissertation is dedicated to my wife, Megan Dittrich-Reed, for her unwavering belief in me. Megan, you are my sunshine.

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Abstract

Understanding processes contributing to the origin of novelty, including ecological transitions in resource or habitat use, is fundamental to evolutionary biology. Early geneticists speculated about the sudden appearance of new species via special macromutations, epitomized by Goldschmidt's infamous "hopeful monster". Transgressive segregation during hybridization is a more plausible mechanism for producing "monstrous" phenotypes beyond the range of parental populations. Transgressive hybrid phenotypes can be products of epistatic interactions or additive effects of multiple recombined loci. However, the importance of hybridization in the origin of novelty is contested because we do not know how often hybridization enhances the probability of an evolutionary transition. In Chapter 1 we compare several epistatic and additive models of transgressive segregation in hybrids and find that they are special cases of a general, classic quantitative genetic model. In Chapters 2 and 3 we take an empirical approach to determine whether hybridization consistently facilitates adaptation to a novel environment by selecting 36 different hybrid crosses among 12 distinct lineages of the red flour beetle (*Tribolium castaneum*) for performance on soy medium. In Chapter 2 we show that hybrid populations adapted to a challenging new environment more rapidly than non-recombinant populations. During 11 generations on soy medium, beetle populations evolved reduced density-dependence, resulting in greater population growth and steady state population size. Change occurred over several generations, and cannot be explained by simple F1 hybrid vigor. Instead, gradual (but rapid) evolutionary change in the ability to thrive in soy was manifested as altered population ecology. In Chapter 3 we show that the developmental rates of hybrid lines increased significantly while non-recombinant lines' developmental rates increased only slightly. Evolution of accelerated developmental rate was not correlated with the evolution of decreased larval density-dependence described in Chapter 2. During the ecological transition to soy, hybridization facilitated adaptation along multiple dimensions, manifested separately at the population and individual levels.

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Introduction

Chapter 1

A major task for evolutionary biology has been to develop and test theories for the origin of novelty that are consistent with the fundamental genetic principles of gradual populational change. Following Pigliucci (2008), we define evolutionary novelty as: new traits, or novel combinations of traits within a lineage that perform a new ecological function and may result in the establishment of new evolutionary lineages. In Chapter 1 we elaborate one mechanism for the sudden origin and evolutionary success of new variants that applies just as well to exceptional size and shape, new color patterns, use of new habitats, and new exons.

Some theorists have invoked special phenomena such as genome-wide "macromutations" (Goldschmidt 1940) or "genetic revolutions" (Mayr 1954) to get around perceived difficulties with the emergence of profound change as the accumulation of subtle changes by the conventional dynamics of mutation, gene flow, drift and selection. However, modern evolutionary theory and empirical research in genetics have consistently reaffirmed the ability of conventional population genetics to explain the origin of new species and phenotypes, and simultaneously exposed flaws in the alternatives (Charlesworth et al. 1982; Lynch 2007). For example, Goldschmidt (1933, 1940) proposed that a novel phenotype must first arise as an instantaneous product of a single “macromutation” or “systemic mutation”. Individuals bearing such macromutations were characterized as “hopeful monsters” by Goldschmidt (1933, 1940). Goldschmidt’s mechanism of speciation was criticized early for being so improbable as to “overtax one’s credulity” (Dobzhansky 1937, p. 53) because of the rarity of the initial mutation of large effect, and the resulting improbability of finding an equally monstrous mate (Dobzhansky 1937).

Recent empirical and theoretical research on hybrid speciation might have revived the hopeful monster in a new, more credible form (Mallet 2007). Often, hybrids produced in segregating populations have higher fitness in novel environments, increasing the likelihood of divergence from parental populations (Arnold and Hodges 1995; Buerkle et al. 2000; Gompert et al. 2006; Karrenberg et al. 2007; Rieseberg et al. 2007; Shahid et al. 2008; Abbott et al. 2010; Fitzpatrick et al. 2010). Arnold and colleagues have promoted the importance of transgressive segregation as the “Evolutionary Novelty” model of hybridization (Arnold 1997; Arnold et al. 1999; Arnold et al. 2012). Mallet (2007) even referred to transgressive hybrids as hopeful monsters, and P. Bateson (1984, 2002) proposed a simple model for the sudden appearance and successful spread of a novel phenotype via hybridization as a mechanism of saltational evolution. It is related to other models of transgressive segregation (Rieseberg et al. 2003) and hybrid fitness (Dobzhansky 1937; Muller 1942; Turelli and Orr 2000). All are special cases of a general multilocus model

(Fitzpatrick 2008) which can give rise to the evolution of novelty or discontinuity as the cumulative or combined outcome of conventional population genetic change.

Chapter 2

For decades, hybridization was generally viewed as maladaptive, resulting in inviable or infertile offspring with little evolutionary potential (Dobzhansky 1937; Muller 1940; Mayr 1942; Coyne and Orr 2004). In contrast, the "Evolutionary Novelty" model predicts that while most early generation hybrid genotypes will have low fitness compared to parental genotypes, a few might have higher fitness, at least in some environments (Anderson 1948; Anderson and Stebbins 1954; Arnold 1997). However, the importance of hybridization in the origin of novelty is contested (see: Arnold 1997; Coyne and Orr 2004; Arnold 2006) because we do not know how often hybridization enhances the probability of an evolutionary transition. In Chapter 2 we take an experimental approach to evaluate whether hybridization consistently promotes rapid adaptation to a challenging new habitat at the population level.

Different models of hybrid fitness and variability have different implications for the trajectory of evolutionary change in populations of hybrid origin. The wide range of recombinant genotypes produced in the F2 and later generations might provide the opportunity for rapid selection of those most fit in the given environment. Populations of hybrid origin that produce high fitness recombinant genotypes might surpass the fitness of both parental lineages. Transgressive hybrids could result from positive interactions between genes with alleles from the different lineages (epistasis), or simply from the additive combination of beneficial alleles at different loci from each parental lineage (Burke and Arnold 2001; Rieseberg et al. 2003; Dittrich-Reed and Fitzpatrick 2012). However, few studies explicitly test the hypothesis that recombinant hybrid lineages might adapt to a challenging environment faster than their parental non-recombinant populations. To our knowledge, only Campbell et al. (2009) explicitly tested whether differences in performance after selection were caused by simple hybrid vigor or increased rate of adaptation. They found that hybrid radish populations had greater response to selection over four generations than either the wild or cultivated species.

In Chapter 2, we ask whether hybrid populations of *T. castaneum* consistently adapt to a challenging novel environment at a different rate from non-recombinant populations. To answer this question we crossed 12 wheat-adapted populations of *T. castaneum* that have remained isolated for 10-200 generations to create 36 hybrid lineages. We maintained non-recombinant and hybrid populations on soy flour medium for 44 weeks (~11 generations) and larvae, pupae, and adults were censused every four weeks beginning on the eighth week. We tested whether hybrid populations adapted to the new diet more rapidly than non-recombinant populations by comparing their population dynamics using both statistical and demographic models. Our data

demonstrate that hybrid lines typically achieve greater population sizes with milder density-dependence than non-recombinant lines. Moreover, this can be explained by faster adaptive evolution rather than simple hybrid vigor.

Chapter 3

In Chapter 3, we take an experimental approach to evaluate whether hybridization frequently promotes rapid adaptation to a challenging new habitat at the individual levels via increased developmental rate. We use developmental rate as a measure of performance in a novel environment. *Tribolium*, like many insects, respond to plastically stress (*e.g.,* a harsh novel diet) by increasing the number of larval instars and decreasing the overall larval developmental rate (Mikel and Standish 1947; Sokoloff et al. 1966; Via and Conner 1995). There is genetic variation in the degree of depression of developmental rate in a stressful environment and, consequently, developmental rate is subject to selection (Bergerson and Wool 1986; Bergerson and Wool 1988; Via 1991; Via and Conner 1995). The evolution of accelerated developmental rate in a novel environment coupled with a loss of performance in the ancestral environment (not necessarily due to a trade-off) could promote diversification through ecological speciation (Schluter 2001).

In Chapter 3, we ask whether hybrid populations of *T. castaneum* evolved faster larval developmental rates relative to non-recombinant populations, demonstrating more rapid adaptation to a stressful novel medium. Results from these experimental populations presented in Chapter 2 demonstrate population-level adaptation in the form of increased demographic rates by the end of the 44 weeks. Hybrid populations tended to evolve more rapidly, with some clearly outperforming their parental lineages. In Chapter 3 we investigate the evolution of individual performance in hybrid vs. non-recombinant populations while controlling for population ecology, and then ask whether individual level and population level measures of performance are correlated. Our data demonstrate that hybrid lines typically evolved faster developmental times than non-recombinant lines. The magnitude of developmental rate evolution was not correlated with change in population level demographic rates, suggesting that they represent distinct dimensions of adaptation. Hybridization tended to enhance adaptation at both population and individual levels, but the signal was more consistent for the individual-level developmental rates.

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Chapter 1: Transgressive hybrids as hopeful monsters

The following chapter is a slightly modified version of an essay the author published in *Evolutionary Biology*:

Dittrich-Reed DR, Fitzpatrick BM. 2013. Transgressive hybrids as hopeful monsters. Evolutionary Biology. 40:310-315.

Abstract

The origin of novelty is a critical subject for evolutionary biologists. Early geneticists speculated about the sudden appearance of new species via special macromutations, epitomized by Goldschmidt's infamous "hopeful monster". Although these ideas were easily dismissed by the insights of the Modern Synthesis, a lingering fascination with the possibility of sudden, dramatic change has persisted. Recent work on hybridization and gene exchange suggests an underappreciated mechanism for the sudden appearance of evolutionary novelty that is entirely consistent with the principles of modern population genetics. Genetic recombination in hybrids can produce transgressive phenotypes, "monstrous" phenotypes beyond the range of parental populations. Transgressive phenotypes can be products of epistatic interactions or additive effects of multiple recombined loci. We compare several epistatic and additive models of transgressive segregation in hybrids and find that they are special cases of a general, classic quantitative genetic model. The Dobzhansky-Muller model predicts "hopeless" monsters, sterile and inviable transgressive phenotypes. The Bateson model predicts "hopeful" monsters with fitness greater than either parental population. The complementation model predicts both. Transgressive segregation after hybridization can rapidly produce novel phenotypes by recombining multiple loci simultaneously. Admixed populations will also produce many similar recombinant phenotypes at the same time, increasing the probability that recombinant "hopeful monsters" will establish true-breeding evolutionary lineages. Recombination is not the only (or even most common) process generating evolutionary novelty, but might be the most credible mechanism for sudden appearance of new forms.

Revival of the hopeful monster

A major task for evolutionary biology has been to develop and test theories for the origin of novelty that are consistent with the fundamental genetic principles of gradual populational change. Novelty, however, is a loaded term with many different definitions that include or exclude a variety of morphological characters (Brigandt and Love 2012). Following Pigliucci (2008), we prefer a more inclusive definition of evolutionary novelty: new traits, or novel combinations of traits within a lineage that perform a new ecological function and may result in the establishment of new evolutionary lineages. More narrowly focused definitions might be desirable for some purposes (Muller and Wagner 1991; Wagner and Lynch 2010). However, our

goal in this essay is to elaborate one mechanism for the sudden origin and evolutionary success of new variants that applies just as well to exceptional size and shape, new color patterns, use of new habitats, and new exons.

Some theorists have invoked special phenomena such as genome-wide "macromutations" (Goldschmidt 1940) or "genetic revolutions" (Mayr 1954) to get around perceived difficulties with the emergence of profound change as the accumulation of subtle changes by the conventional dynamics of mutation, gene flow, drift and selection. However, modern evolutionary theory and empirical research in genetics have consistently reaffirmed the ability of conventional population genetics to explain the origin of new species and phenotypes, and simultaneously exposed flaws in the alternatives (Charlesworth et al. 1982; Lynch 2007). For example, Goldschmidt (1933, 1940) proposed that a novel phenotype (such as insect wings, a character associated with higher level taxonomy) must first arise as an instantaneous product of a single “macromutation” or “systemic mutation”. Individuals bearing such macromutations were characterized as “hopeful monsters” by Goldschmidt (1933, 1940) to emphasize that their appearance is neither purposeful nor gradual, and their prospects for success are a matter of luck. A hopeful monster is an individual phenotypically discontinuous from the range of phenotypes of its population, and whose hopes of establishing a new lineage lie in finding a novel niche for which its monstrosity happens to be preadapted. Such a mechanism of speciation was criticized early for being so improbable as to “overtax one’s credulity” (Dobzhansky 1937, p. 53) because of the rarity of the initial mutation of large effect, and the resulting improbability of finding an equally monstrous mate (Dobzhansky 1937).

Recent empirical and theoretical research on hybrid speciation might have revived the hopeful monster in a new, more credible form (Mallet 2007). Recombination of parental chromosomes in the F2 and later generations during hybridization can generate genotypes that express phenotypes outside the normal range of variation observed in either parental gene pool, a phenomenon termed “transgressive segregation” (Figure I-1; Rieseberg et al. 1999; Rieseberg et al. 2003; Rosenthal et al. 2005; Johnson et al. 2010; Parsons et al. 2011). Often, transgressive hybrids have higher fitness in novel environments, increasing the likelihood of divergence from parental populations (Arnold and Hodges 1995; Buerkle et al. 2000; Gompert et al. 2006; Karrenberg et al. 2007; Rieseberg et al. 2007; Shahid et al. 2008; Abbott et al. 2010; Fitzpatrick et al. 2010). A few examples of new phenotypes inferred to arise from hybridization include (see Arnold 1997; Arnold 2006; Stelkens and Seehausen 2009 for more exhaustive reviews): extreme size of tiger x lion F1 hybrids (Gray 1954); unique shapes and colors of hybrid orchids (Rolfe and Hurst 1909); ability of recombinant sunflowers to thrive in extreme habits (Lexer et al. 2003; Rieseberg et al. 2003; Rieseberg et al. 2007); specialization on a novel host plant in lonicera flies (Schwarz et al. 2005); and expression of novel gene transcripts (including new exons) via alternative splicing in hybrid poplars (Scascitelli et al. 2010). Not all specific examples are relevant in nature, and not

all would qualify as “evolutionary novelty” under certain definitions (Muller and Wagner 1991; Pigliucci 2008; Wagner and Lynch 2010), but this small selection of cases serves to illustrate sudden appearance of profound differences between parents and hybrid offspring reminiscent of Goldschmidt’s hopeful monsters.

Arnold and colleagues have promoted the importance of transgressive segregation as the “Evolutionary Novelty” model of hybridization (Arnold 1997; Arnold et al. 1999; Arnold et al. 2012). Mallet (2007) even referred to transgressive hybrids as hopeful monsters, and P. Bateson (1984, 2002) proposed a simple model for the sudden appearance and successful spread of a novel phenotype via hybridization as a mechanism of saltational evolution. We expand and make genetically explicit the haploid, diploid and polyploid cases of his model (Figure I-2). It is related to other models of transgressive segregation (Rieseberg et al. 2003) and hybrid fitness (Dobzhansky 1937; Muller 1942; Turelli and Orr 2000). All are special cases of a general multilocus model (Fitzpatrick 2008) which can give rise to the evolution of novelty or discontinuity as the cumulative or combined outcome of conventional population genetic change. Indeed, recombination has always been recognized as an important source of variation (Mendel 1866); whether such variation is perceived as profound or "monstrous" is a matter of degree rather than kind.

The Bateson Model

Bateson's (1984, 2002) proposal for how recombination can generate sudden change is a straightforward narrative. Two different mutations (*A* and *B*) appear and become fixed in different populations with similar phenotypes (circles in his diagram). When the populations merge, recombinant individuals with both *A* and *B* express a new phenotype (diamonds in his diagram), which is more successful and becomes fixed. Aside from “mutation”, Bateson did not use genetically explicit vocabulary, but his diagram suggests a haploid genome, with mutations *A* and *B* occurring in different loci such that recombination can place them together in the same individual. We show a version of Bateson's model with explicit haploid, diploid, and allopolyploid cases in Figure I-2. The key feature is that the new phenotype depends on the interaction between alleles *A* and *B* at different loci. If both *A* and *B* alleles are common in the admixed population, the new phenotype will be expressed by a large number of individuals who can interbreed with each other, rather than a single mutant monster with no prospect for a mate. Moreover, even if interactions at other loci render some hybrids (even F1 hybrids) partly or mostly sterile, recombination could produce transgressive hybrids with restored fertility in the F2 and later generations (Figure I-3).

The General Model

Bateson (2002) went on to note that his idea had "points of similarity" with the Dobzhansky-Muller model of hybrid dysfunction (Dobzhansky 1937; Muller 1942; Turelli and Orr 2000) and the earlier verbal model of W. Bateson (1909). In fact, the explicit diploid version of Bateson's model differs from the Dobzhansky-Muller model only in the sign of the interaction: The Bateson model supposes the interaction between *A* and *B* increases fitness, while the Dobzhansky-Muller model specifies a decrease in fitness of recombinant hybrids (Tables I-1A & I-1B). Both models describe gene interaction (epistasis) causing a hybrid phenotype to fall outside the range for either parental population. That is, they are special cases of transgressive segregation.

Transgressive segregation can also be caused by strictly additive effects of multiple genes (Table 1C; Nilsson-Ehle 1911; Grant 1975). This is the genetic model favored by Rieseberg et al. (2003) because in QTL studies of transgressive hybridization in plants, additive effects are detected more often than epistatic or dominance interactions (Rieseberg et al. 1999). Strictly additive and strictly epistatic models are special cases of the general quantitative genetic model allowing phenotypes to be affected by additive, dominance, and epistatic effects (Hill 1984; Lynch and Walsh 1997; Fitzpatrick 2008). Extending these basic ideas to many loci and multivariate phenotypes leads to the very general conclusion that recombination between disparate genomes has great potential to produce novel phenotypes (Gavrilets 1999).

Predictions

The primary prediction characterizing many years of speciation research is that hybridization between disparate genomes will often generate novel phenotypes that are inviable or sterile (“hopeless monsters”), and this becomes ever more likely with increasing differentiation (Dobzhansky 1937; Mayr 1942; Muller 1942; Orr and Turelli 2001; Coyne and Orr 2004; Gavrilets 2004). At the same time, the number of potentially beneficial interactions might increase (Stelkens and Seehausen 2009; Stelkens et al. 2009), leading to a race between the potential for hybrid speciation and the evolution of complete reproductive isolation. Here, as in the case of mutations of large effect, there is probably an inverse relationship between the magnitude of a transgressive beneficial phenotype and the likelihood that it will actually be generated in nature.

The most important prediction arising from hybridization as a source of novelty is that admixed populations with many recombinant individuals repeatedly bring together many genetic differences in many unique combinations. These two key features can facilitate rapid adaptive evolution of a new phenotype. First, instead of a single genetic difference, the diversity of

recombinant genotypes after the F1 generation provides a wide field for selection of beneficial vs. deleterious interactions (Lexer et al. 2003; Parsons et al. 2011). As pointed out by Arnold and Hodges (1995), this means that even if most hybrid interactions are deleterious, there is still a good chance for the rare beneficial recombinant to appear, unless F1 hybrids are completely sterile or inviable. Second, segregating hybrid populations will repeatedly produce recombinant genotypes with transgressive phenotypes (Figures I-2 & I-3), instead of only producing a single unique mutant or rare variant likely to be lost, even if advantageous (Gillespie 2004). This means hopeful monsters produced by transgressive segregation have a good chance of finding suitably monstrous mates in a hybrid population and can establish a true-breeding population derived from many independent interspecific matings (Bateson 2002).

Although speciation by transgressive hybridization is expected to be rapid in diploids (Ungerer et al. 1998), we predict fixation of novel transgressive hybrids to be more rapid and perhaps more common in haploid and allopolyploid hybrids. All of the recombinant hybrids in haploid and allopolyploid populations will be true-breeding, compared to just a fraction of diploid recombinant hybrids (Figure I-2). In the case of complete or incomplete dominance of *A* and *B*, all four diploid recombinant genotypes will exhibit a transgressive phenotype, but only the double homozygote will be true-breeding. This might lead to lower average fitness of a diploid hybrid population that contains some high-fitness transgressive phenotypes for several generations after hybridization is initiated (Johnson et al. 2010).

Finally, other more subtle predictions might arise from variation in genomic structure and development. For example, the Dobzhansky-Muller model helps explain empirical generalizations including Haldane's Rule and the large-X effect in hybrid dysfunction. By extension, the expression of beneficial transgressive phenotypes might differ between sex chromosomes and autosomes, with differential consequences for males and females in lineages with chromosomal sex determination. Specifically, if transgressive phenotypes are often recessive ($s_0 < ½\ s_1 < ½\ s_2$ in Table I-1B) and one or more of the interacting genes is on the sex chromosome, then the phenotype is more likely to be expressed in the heterogametic sex, even in the F1 generation. Whether such "rules" might exist for transgressive phenotypes depends largely on whether dominance is a consistent effect in trait expression. The only broad generalization emerging from reviews of the empirical literature so far appears to be that the additive complementation model is often adequate to explain the data (Rieseberg et al. 1999; Burke and Arnold 2001). However, epistasis and dominance are not infrequently detected, and the difference might reflect lower statistical power to detect non-additive effects.

Conclusions

The idea that hybridization can rapidly produce novel forms is familiar among botanists, but rarely appeared in mainstream discussions of speciation until recently thanks to several case studies of homoploid hybrid speciation (for reviews see: Arnold 1997; Rieseberg et al. 1999; Rieseberg et al. 2003; Arnold 2006; Mallet 2007). Recombination of fixed genetic differences between two populations in the F2 and later generations can produce hybrids with phenotypes novel to both parental populations (Figure I-3). When these recombinant phenotypes have fitness beyond the range of parental phenotypes they are transgressive (Figure I-1).

Bateson's model of hybridogenic hopeful monsters and the Dobzhansky-Muller incompatibility model of hybrid inviability are both cases of transgressive segregation. The Dobzhansky-Muller model produces a "hopeless monster": hopeless because sterility and inviability make finding a mate and/or novel niche moot and monstrous because sterility and inviability are both phenotypes outside the parental range of phenotypes (Table I-1A). The Bateson model produces a hopeful monster: hopeful because it has a good chance of finding a mate given continued hybridization and greater fitness than parental phenotypes in some environments, and monstrous because of its transgressive phenotype (Table I-1B). The complementation model can produce both (Table I-1C). All three models are special cases of the general quantitative genetic model, thus reconciling sudden and gradual origins of novelty without requiring a special class of mutations or population dynamics.

Transgressive segregation might be an important mechanism promoting sudden phenotypic changes and ecological transitions in evolution. Even if most of the variation produced is deleterious, a rare transgressive hybrid genotype could rapidly fix in a population or establish a novel lineage. It is even possible that regularities in the distribution of dominance effects could lead to general predictions (such as the large X effect and Haldane's Rule) for transgressive trait expression, but more research on the genetic architecture of transgressive traits is needed. Regardless of those details, admixture can simultaneously bring together many new combinations of alleles, generating multilocus novelties that might never have appeared via gradual accumulation of new mutations in a single population. Gene exchange is not the sole, nor even necessarily most likely, source of evolutionary novelty (Meyer 2002; Moczek 2008), but is perhaps the most likely mechanism of sudden, population level change. Transgressive segregation might be just the mechanism to make more monsters hopeful.

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Appendix I. Figures and Tables

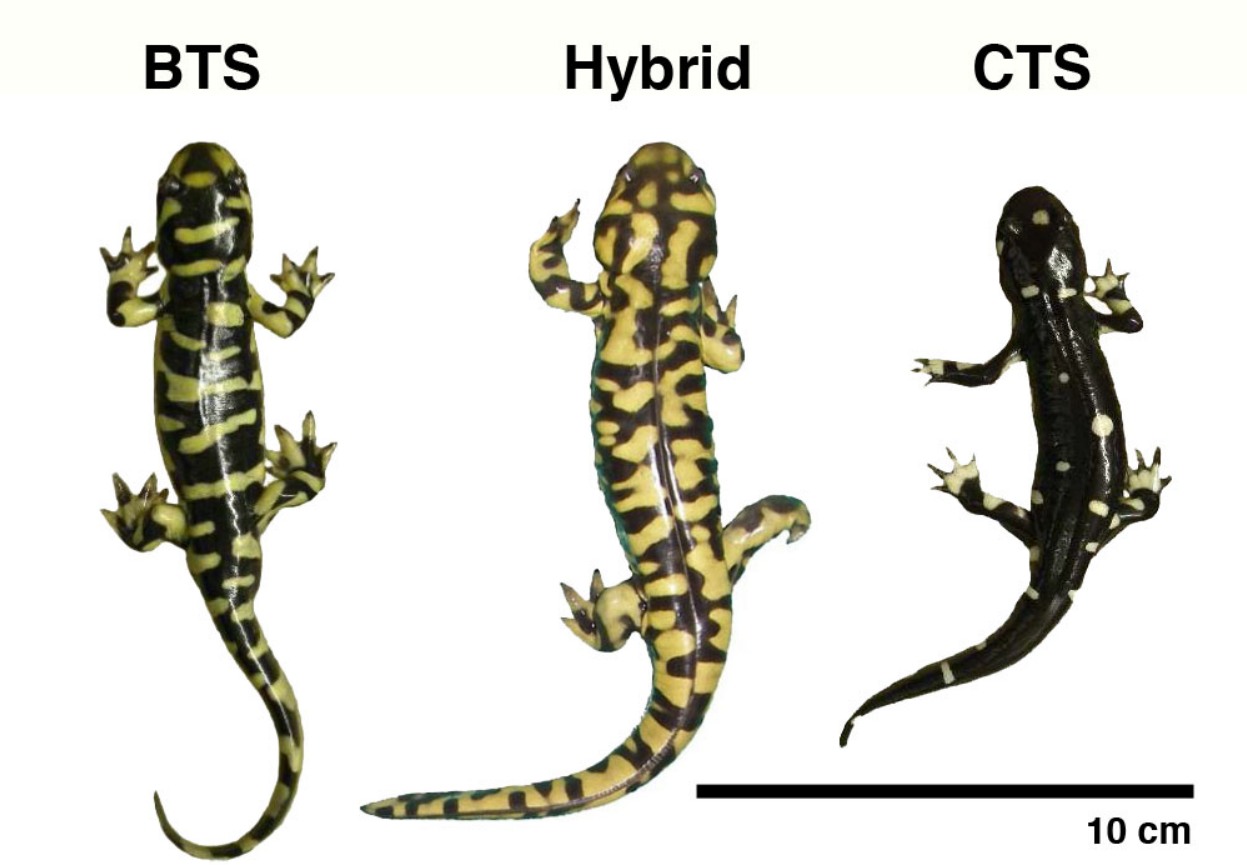

Figure I-1. An example of transgressive segregation in a hybrid population with *Ambystoma*. Recently metamorphosed juvenile tiger salamanders representative of *Ambystoma mavortium* (BTS), *A. californiense* (CTS) and transgressive later generation hybrid. The late generation hybrid has both a transgressive coloration and body size (mass and snout-vent length) beyond the range of parental populations.

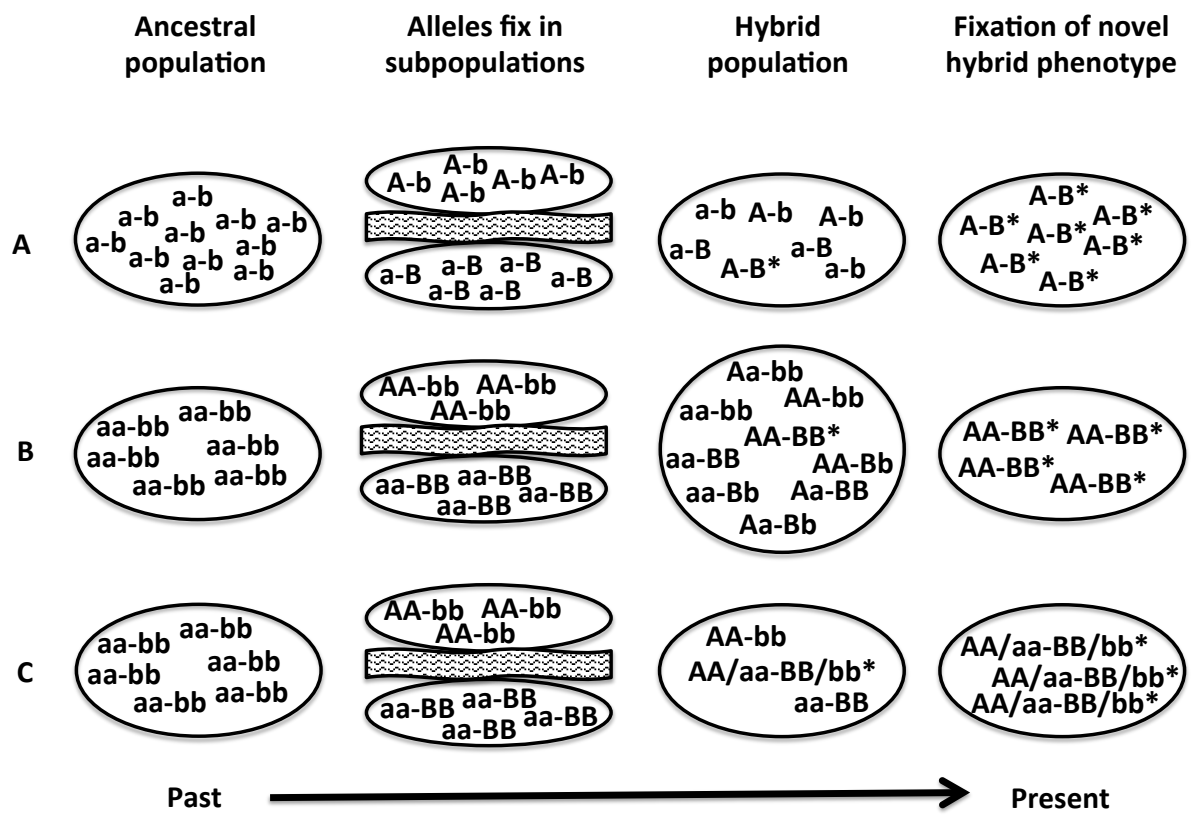

Figure I-2. Genetically explicit versions of Bateson's model. (A) The haploid case, (B) the diploid case, (C) allopolyploidy. Genotypes with asterisks are novel recombinant, true-breeding genotypes.

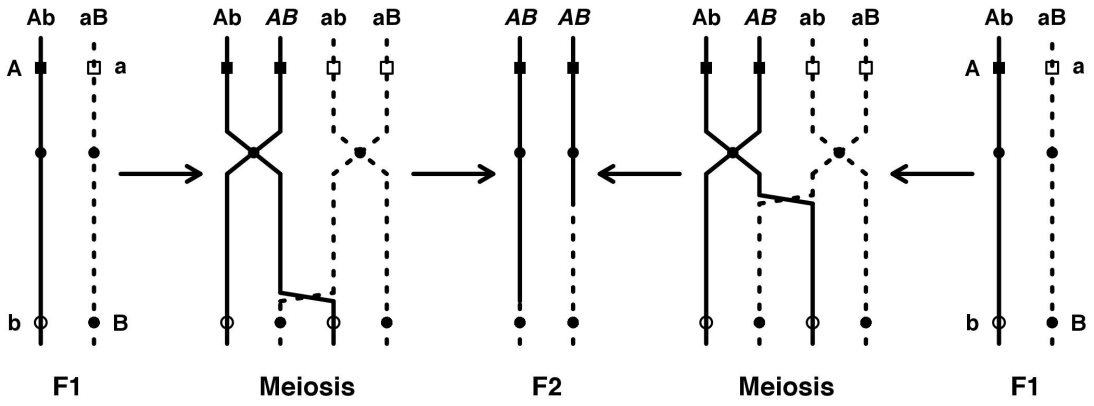

Figure I-3. Recombination in the F2 generation. A schematic representation of the process by which two fixed allelic differences (A and B) at unlinked loci might recombine during meiosis in two F1 hybrids to create a novel homozygous genotype (AABB) in the F2 hybrid. Solid and dashed chromosome patterns are indicative of population ancestry. Note that the two novel recombinant chromosomes in the F2 are the result of independent recombinational events.

Table I-1. Diploid, two-locus models for hybrid phenotypes. In each case, parental genotypes are AAbb aaBB. Epistatic hybrid dysfunction (A: the Dobzhansky-Muller model) and epistatic hybrid vigor (B: the Bateson model) differ only in whether effects are assumed to be deleterious or beneficial. The additive complementation model (C) shows how recombinants can be phenotypically extreme relative to parentals (AAbb and aaBB) even without gene interaction (each A or B allele contributes an amount x to the phenotypic value, regardless of the other locus). All can be written as special cases of a general quantitative genetic model (Hill 1984; Lynch and Walsh 1997; Fitzpatrick 2008).

	aa	Aa	AA
bb	1	1	1
Bb	1	$1 - h_0$	$1 - h_1$
BB	1	$1 - h_1$	$1 - h_2$

(A)

	aa	Aa	AA
bb	1	1	1
Bb	1	$1 + s_0$	$1 + s_1$
BB	1	$1 + s_1$	$1 + s_2$

(B)

	aa	Aa	AA
bb	$1 - 2x$	$1 - x$	1
Bb	$1 - x$	1	$1 + x$
BB	1	$1 + x$	$1 + 2x$

(C)

Chapter 2: Hybridization increases rate of adaptation to novel environment

Abstract

Understanding processes contributing to the origin of novelty, including ecological transitions in resource or habitat use, is fundamental to evolutionary biology. Although evolutionary novelty ultimately depends on mutations and how they interact with developmental systems and the environment, hybridization might dramatically affect the appearance and population dynamics of novel traits. However, the importance of hybridization in the origin of novelty is contested because we do not know how often hybridization enhances the probability of an evolutionary transition. Here we show that hybrid populations adapted to a challenging new environment more rapidly than non-recombinant populations in an experiment using 36 different hybrid crosses among 12 distinct lineages of the red flour beetle (*Tribolium castaneum*). During 11 generations on soy flour, adaptation generally had the effect of reducing density-dependence, resulting in greater population growth and steady state population size. Change occurred over several generations, and cannot be explained by simple F1 hybrid vigor. Instead, gradual (but rapid) evolutionary change in the ability to thrive in soy was manifested as altered population ecology. Thus, hybridization promoted adaptation via evolutionary-ecological dynamics during the transition to a challenging novel environment.

Introduction

For decades, hybridization was generally viewed as maladaptive, resulting in inviable or infertile offspring with little evolutionary potential (Dobzhansky 1937; Muller 1940; Mayr 1942; Coyne and Orr 2004). In contrast, the "Evolutionary Novelty" model predicts that while most early generation hybrid genotypes will have low fitness compared to parental genotypes, a few might have higher fitness, at least in some environments (Anderson 1948; Anderson and Stebbins 1954; Arnold 1997). These high fitness recombinants might become established as evolutionarily independent lineages with novel ecological characteristics. This conceptual model is supported by computer simulations (Buerkle et al. 2000; Barton 2001; Duenez-Gusman et al. 2009) and some case studies of natural and experimental hybridization in plants and animals (Rieseberg et al. 2003; Schwarz et al. 2005; Gompert et al. 2006; Mavarez et al. 2006; Agashe et al. 2011). However, the importance of hybridization in the origin of novelty is contested (see: Arnold 1997; Coyne and Orr 2004; Arnold 2006) because we do not know how often hybridization enhances the probability of an evolutionary transition from one environment to another. While hybridization is not uncommon in nature (Anderson and Stebbins 1954; Arnold 1997; Rieseberg 1997), its apparent association with a particular adaptive change might be incidental. Moreover, hybridization often results in hybrid dysfunction, leading to doubts about the evolutionary potential of hybrid genotypes (Dobzhansky 1937; Coyne and Orr 2004). Here we take an experimental approach to evaluate whether hybridization consistently promotes rapid adaptation to a challenging new habitat.

Different models of hybrid fitness and variability have different implications for the trajectory of evolutionary change in populations of hybrid origin (Figure II-1). A naïve expectation might be strict intermediacy of hybrid populations, even as they gradually become more adapted to a novel habitat (Figure II-1A). More likely, the wide range of recombinant genotypes produced in the F2 and later generations will provide the opportunity for rapid selection of those most fit in the given environment. One possibility is "evolutionary dominance" (Figure II-1B), in which one parental lineage carries superior alleles at all relevant loci. Natural selection is expected to result in the fixation of those alleles, effectively recovering the superior parental phenotype from the hybrid gene pool. In contrast, the "Evolutionary Novelty" model predicts positive "transgressive evolution" (Figure II-1B), in which populations of hybrid origin come to surpass the fitness of both parents because some recombinant genotypes have higher fitness and greater evolutionary potential than either parental lineage. This transgression could result from positive interactions between genes with alleles from the different lineages (epistasis), or simply from the additive combination of beneficial alleles at different loci from each parental lineage (Burke and Arnold 2001; Rieseberg et al. 2003; Dittrich-Reed and Fitzpatrick 2012). Obviously, severe hybrid dysfunction might result in extinction or rapid elimination of one parental gene pool from a local population. Moreover, in complex gene pools, like hybrid populations, it is also possible for an antagonism between selection and recombination to make natural selection rather inefficient and allow low fitness recombinant genotypes to linger or recur, especially when selection is epistatic (Barton and Keightley 2002; Johnson et al. 2010). Thus, the rate of adaptation in hybrid lineages might be great, but might also be subject to significant constraints or lags depending on the genetic basis of fitness variation. Therefore, a multiple generation study is necessary to determine the outcome of adaptation of hybrid lineages to a novel environment.

Few studies explicitly test the hypothesis that recombinant hybrid lineages might adapt to a challenging environment faster than their parental non-recombinant populations. Hercus & Hoffmann (1999), found no difference in fitness between interspecific *Drosophila* hybrids and their parental species after 30 generations of selection in a stressful environment. Lewontin & Birch (1966) working with hybrid *Dacus* flies and Nagle & Mettler (1969) working with hybrid *Drosophila* flies showed differences in performance between hybrid and non-recombinant lines after multiple generations of selection. Agashe et al. (2009; 2011) found a negative correlation between degree of admixture and extinction risk on a challenging medium (corn) in *T. castaneum*. However, only Campbell et al. (2009) explicitly tested whether differences in performance after selection were caused by simple hybrid vigor or increased rate of adaptation. They found that hybrid radish populations had greater response to selection over four generations than either the wild or cultivated species.

In this article, we ask whether hybrid populations of *T. castaneum* consistently adapt to a challenging novel environment at a different rate from non-recombinant populations. To answer this question we crossed 12 wheat-adapted populations of *T. castaneum* that have remained isolated for 10-200 generations to create 36 hybrid lineages (see Methods below; Table II-2). We maintained non-recombinant and hybrid populations on soy flour medium for 44 weeks (~11 generations) and larvae, pupae, and adults were censused every four weeks beginning on the eighth week. We tested whether hybrid populations adapted to the new diet more rapidly than non-recombinant populations by comparing their population dynamics using both statistical and demographic models. Our data demonstrate that hybrid lines typically achieve greater population sizes with milder density-dependence than non-recombinant lines. Moreover, this can be explained by faster adaptive evolution rather than an initial demographic advantage from hybrid vigor.

Methods

Model system

Tribolium castaneum (Coleoptera, Tenebrionidae), red flour beetles, are ideal models for testing hypotheses in evolutionary biology. *Tribolium castaneum* are easy to maintain and census in the laboratory, have a relatively simple ecology, a relatively short generation time, and sexual reproduction (Sokoloff 1972). They are ideal for studies of the effects of hybridization because failure rates of interpopulation crosses vary with geographic distance of source localities, but have not been observed to exceed 10% (Demuth and Wade 2007). Moreover, *T. castaneum* are excellent for studying adaptation to new environments because populations differ in performance on different media (Via 1991). Development is slower in media with low nutrient quality or high toxicity (Sokoloff et al. 1966), but is subject to selection and can increase dramatically after ten to fifteen generations of selection (Bergerson and Wool 1988). Likewise, fecundity and survival decrease with decreasing nutrient quality or increasing toxicity, but will also respond to selection (Bergerson and Wool 1988; Agashe et al. 2011).

Tribolium castaneum are cosmopolitan pests of stored food products, especially in tropical and subtropical latitudes (Sokoloff 1972). The beetles used in this experiment were all originally collected from stored grain making a container of grain ecologically relevant mesocosm. Whole wheat flour supplemented with brewer's yeast, inactive *Saccharomyces cerevisiae*, is the standard medium for *Tribolium* culture and the "ancestral environment" for this study. Soy flour medium, the "novel environment", increases developmental time and number of larval instars (Mikel and Standish 1947), inhibits protein digestion (Lipke et al. 1954), and decreases productivity (Sokoloff et al. 1966).

Parental lines

The twelve *T. castaneum* strains that founded our experimental populations were originally collected from four continents and found originally on one of three different grains (Table II-1). We obtained six strains from R. Beeman at the Center for Grain and Animal Health Research, ARS-USDA, Manhattan, KS. We received an additional five strains from J. Demuth at the University of Texas, Arlington. The final strain was provided by J. Mathias at the Rich Products Corporation facility in Murfreesboro, TN. Since collection, all strains have been maintained on standard *Tribolium* medium (95% whole wheat, 5% Brewer's yeast). Since 2010, all strains have been maintained at 34 C, 45% r.h., and on a 12 hr light cycle.

Experimental lines

We initiated non-recombinant populations with ten male and ten female pupae from a single parental strain. We initiated hybrid populations with ten male and ten female pupae from two different parental strains. Each parental strain was a contributor for six hybrid cross-types, three times as the maternal contributor and three times as the paternal contributor. We did not generate reciprocal crosses. For each of the 36 hybrid and 12 non-recombinant cross-types we initiated 5 replicates for a total of 240 experimental populations (Table II-2).

Novel environment

We wanted to determine whether hybrid or non-recombinant populations would be able to adapt to a novel environment more rapidly. Soy flour is both a novel and selective environment. Soy (*Glycine max*) is one of the few non-poaceous commercial flour products *T. castaneum* might encounter and none of the parental strains have any known history of exposure to soy flour. *Tribolium castaneum* maintained on soy flour experience reduced larval recruitment developmental rate (Mikel and Standish 1947; Sokoloff et al. 1966; Imura 1991), possibly due to inhibition of protein digestion (Lipke et al. 1954).

Each experimental replicate population was maintained on 10 mL of soy-flour medium (95% soy flour, 5% Brewer's yeast; ca. 4g) in 7 dram amber containers and censused every four weeks (approximately one generation) from week 8 through week 44. At each census, beetles were sifted from the medium using a #20 sieve and adults, pupae, and larvae were photographed and then placed on fresh medium. Six females were removed to assay the developmental rate of their offspring on wheat and soy media (data to be presented elsewhere), and returned the following day.

Population size dynamics

Time series analysis – To compare average population fitness over time of hybrid and non-recombinant lines, we tested whether for changes in population density. We asked whether population density could be described by a single statistical model (regardless of hybrid or non-

recombinant origin) or one with separate parameters for hybrid and non-recombinant populations. We fit generalized additive mixed models (GAMMs) with one cubic regression spline smoothers for all time series or two smoothers (one for hybrid population time series, one for non-recombinant population time series). We compared models with and without hybrid status as a fixed effect (Table II-3) using AICc; Akaike's Information Criterion corrected for sample size (Burnham and Anderson 2004). We included paternal strain, cross type, and replicate as nested random effects. Including maternal strain as an additional random effect did not account for variance over and above paternal strain and cross type. To account for temporal autocorrelation, all models included a first order autoregressive correlation structure. This analysis assesses non-linearity of population size change over time and accounts for non-independence owing to both temporal autocorrelation (within populations) and shared ancestry (among populations). We used log-transformed population density to increase normality of residuals. We also allowed for different residual variances to be estimated for hybrid and non-recombinant lines and certain census periods with high and low residual variance to relax the model assumption of homoscedasticity of residuals (Zuur et al. 2009). Models were fit via restricted maximum likelihood using the *gamm* function of the *mgcv* package in R (Wood 2004).

In other words, the GAMM for y_{ijks}, the log population size of replicate i, cross type j, and paternal line k during census period s is

$$\begin{aligned} y_{ijks} &= \alpha + \beta\,\mathrm{Hybrid}_j + f_h\,(\mathrm{Census}_s) + a_k + a_{jk} + a_{ijk} + \varepsilon_{ijks} \\ \varepsilon_{ijks} &\sim \mathrm{N}(0, \sigma^2_{h,s}) \\ \mathrm{cor}(\varepsilon_{ijks}, \varepsilon_{ijkt}) &= \rho^{|t-s|} \end{aligned} \qquad (1)$$

where α is the intercept, β is the fixed effect of the hybrid status (hybrid or non-recombinant) of cross type j, f_h (Census$_s$) are smoothing functions for the time series data (s is census period 0 through 11) for hybrid and non-recombinant lines (h), a_k is the random intercept for paternal line, a_{jk} is the random intercept for cross type, a_{ijk} is the random intercept for replicate (within a time series), and ε_{ijks} is the randomly distributed error with mean 0, and variance σ^2. Residual variance σ^2 was estimated for hybrid and non-recombinant lines (h) and census periods with high (s = 2, 5) and low (s = 0, 3-4, 6-11) residual variance to allow for heterogeneity of residual variance in the model. Additionally, ρ is the correlation coefficient for the correlation between residuals at census s and census t.

Overall change in population size – As a simpler comparison of overall change in population size of hybrid and non-recombinant populations, we tested whether the change in population size was best described by a single statistical model, or one with separate parameters for hybrid and non-recombinant populations. We used the natural log of the ratio of population size of the final census (week 44) to the initial census (week 0) rather than the raw difference

between final and initial population sizes as the response to meet assumptions of normality and homoscedasticity of the residuals. We calculated the model-averaged estimate of the hybrid effect and its unconditional variance (Anderson 2008). We accounted for non-independence among populations due to shared ancestry by fitting random intercepts for paternal strain and experimental line. We used a variance structure that allowed different variances for hybrid and non-recombinant lineages to relax the model assumption of homoscedasticity of residuals. To meet the model assumption of normality of residuals, we performed a 95% Winsorization on the data.

The full model is:

$$\Delta y_{ijk} = \alpha + \beta\ \text{Hybrid}_j + a_k + a_{jk} + \varepsilon_{ijk} \qquad (2)$$
$$\varepsilon_{ijk} \sim N(0, \sigma^2_h),$$

where Δy_{ijk} is the (Winsorized) change in log population size, and the explanatory terms are the same as Eq. 1. Models were fit using the *lme* function of the *nlme* package in R (Pinheiro et al. 2012).

Change in population size by cross type – To determine whether the change in population size of a particular hybrid line was most consistent with hybrid intermediacy, evolutionary dominance, or transgressive evolution, we compared models analogous to quantitative genetic models of additivity, dominance, and transgression for each of hybrid and the experimental lines founded by the hybrid's two parental strains (Lynch and Walsh 1998; Table II-4). Additive effects of parental genomic contributions to overall population change would result in hybrid populations that grew an amount intermediate to non-recombinant "parental" populations. Evolutionary dominance predicts hybrid population growth more similar to one non-recombinant "parental" line than the other. Transgressive evolution would result in hybrid populations outperforming both parents.

We fit six linear models to the population size data for each case study, with different combinations of parameters for additivity, dominance, and hybrid status and calculated the model probabilities (weights) for each model (Anderson 2008; Table II-4). We combined model weights for subsets of models that provided evidence for the same hypothesis (e.g., weights for models 5 and 6 would be combined to determine the strength of evidence for transgression, see Table II-4). The hypothesis with the most support (greatest combined model weight) was considered to be the best interpretation of the data for a given case study. We also examined the range of population change for each line in the case study to confirm our interpretations. Additionally we recorded the number of hybrid populations with population size change beyond the range of populations of either "parental" line.

Change in demographic parameters

The LAT model - Increases in population size might be the product of adaptation, but they might also be caused by normal population dynamics in the absence of evolutionary change. We tested whether changes in population density were consistent with a standard density-dependent population model (without evolution) or one in which demographic parameters were allowed to evolve over the 44 week experiment. We fit nonlinear population dynamic models with constant and time-dependent demographic parameters to determine whether the data provide evidence of adaptation. Dennis et al. (1995) used a set of nonlinear difference equations (the "LPA model"; "Larva, Pupa, Adult") to model the population dynamics of *T. castaneum* in a constant environment over multiple generations. We modified the LPA model to better fit our census protocol by changing the period time from two weeks to four and subsequently collapsing the pupal and adult age classes due to the increase in period. Our modification of the LPA model, the "LAT model" ("Larva, Adult, Time"), is a system of two nonlinear difference equations for calculating the number of larvae (L) and sum of pupae and adults (A; henceforth referred to simply as "adults") at time t+1 from L and A at time t:

$$L_{t+1} = b(1 + \Delta b)^t A_t \exp[-c_{ea}(1 + \Delta c_{ea})^t A_t - c_{el}(1 + \Delta c_{el})^t L_t] \quad (3)$$

$$A_{t+1} = L_t[1 - \mu_l(1 + \Delta\mu_l)^t] + A_t[1 - \mu_a(1 + \Delta\mu_a)^t] \quad (4)$$

Time t is in units of four-week census periods, approximately one generation time. The quantity $b \geq 0$ is the average number of larvae produced per adult and $\Delta b \geq 0$ is the rate of adaptation for b. The exponential term in Eq. 3 is the probability that an egg survives the combined density-dependent effects of larvae and adults, labeled "cannibalism" by Dennis et al. (1995). The coefficients c_{ea} and $c_{el} \geq 0$ determine the strength of the density-dependent effects of adults and larvae on recruitment and Δc_{ea} and Δc_{el} are the rates of change for c_{ea} and c_{el}. The fractions μ_l and μ_a are the mortality probabilities for larvae and adults and $\Delta\mu_l$ and $\Delta\mu_a \leq 0$ are the rates of adaptation for μ_l and μ_a.

Model fitting and parameter estimation – In order to determine whether changes in population size were explained by unchanging or evolving demographic parameters, we fit nine different LAT models to the time series data for each line (pooling between 1 and 5 replicate populations). These LAT models allowed all, some, or none of the adaptation rate parameters to vary (Table II-5). Following Dennis et al. (1995), we optimized demographic parameters using conditional least squares using the *optim* function in R (R Core Team 2012). Conditional least squares optimization was more efficient than likelihood optimization, which often failed to converge. We then calculated the likelihood of the data given the optimized parameter set and the AICc for each model to compare models with and without rate parameters. Due to

uncertainty in model selection, the demographic parameters estimated for each of the nine models were also model-averaged for each line (Anderson 2008).

Hybridization and change in demographic parameters – To determine whether hybrid or non-recombinant lines adapted faster, we used linear mixed models to test whether model-averaged adaptation parameter estimates were consistently different between hybrid and non-recombinant lines. We accounted for non-independence among populations due to shared ancestry by fitting random intercepts for maternal strain. We used a variance structure that allowed different variances for hybrid and non-recombinant lineages to relax the model assumption of homoscedasticity of the residuals. Due to the influence of outliers, we performed a 99% Winsorization on the data. The model fit for each adaptation rate parameter Δx for cross type j and maternal line k is

$$\Delta x_{jk} = \alpha + \beta \, \text{Hybrid}_j + a_k + \varepsilon_{jk} \qquad (5)$$
$$\varepsilon_{jk} \sim N(0, \sigma^2_h)$$

where Δx is one of the five (Winsorized) adaptation rate parameters (Δb, Δc_{ea}, Δc_{el}, $\Delta \mu_l$, $\Delta \mu_a$), and explanatory variables are the same as in Eq. 1, except the subscript k refers to the maternal line. Models were fit using the *lme* function of the *nlme* package in R (Pinheiro et al. 2012).

Body size and population density

To determine whether increases in population size might be caused by early pupation due to malnutrition or crowding (Jackman and Haynes 1975; Peters and Barbosa 1977), we measured the body size of a sample of ten adults of seven of the highest and lowest performing lineages for three census periods (weeks 8, 16, and 44). Body size was calculated as the product of the elytral suture length and anterior elytral margin width. We measured adult beetles photographed during the census using ImageJ software (Rasband 1997-2012). To test whether time and population size affected body size, we compared a linear mixed model with time and population size as fixed effects to one without fixed effects. Both models included random intercepts for population. The model without fixed effects was strongly preferred to the model with body size and time as fixed effects (ΔAICc = 18.18, w = 0.9999). Therefore, there was no evidence that body size changes with time or population size, and we did not pursue the relationship further. Models were fit using the *lme* function of the *nlme* package in R (Pinheiro et al. 2012).

Population persistence

To determine whether non-recombinant lineages were more likely to go extinct than hybrid lineages, we tested whether population extinction was best described by a single model or one with separate parameters for hybrids and non-recombinants. We fit Cox survival models with and without hybrid status as a fixed effect. We included nested random intercepts for paternal

strain, experimental line, and population to account for shared ancestry. We evaluated the support for each model with AICc values. Models were fit using the *coxme* function of the *coxme* package (Therneau 2012).

Of the 240 initial lineages, 29 lineages went extinct (11 non-recombinant and 18 recombinant lineages) and three were removed due to cross-contamination or missing data. There was little support for the model including hybrid status as a fixed effect (ΔAICc = 0.217). Although the model-averaged estimate of the risk of extinction for a non-recombinant population was 1.44 times higher, there was no support for a difference in extinction risks (95% CI = 0.643 – 3.247). That is, most of the variation in extinction risk seems to be explained by the additive effects of parental lineage (mostly parental line "L" Table II-1), with hybrid lines tending to be intermediate. Our result is much weaker than that of Agashe (2009), who observed both a higher extinction rate in *T. castaneum* maintained on an atypical diet (corn) and a positive relationship between population persistence and degree of founding admixture.

All analyses were conducted in R (v. 2.15.2; R Core Team 2012). AICc values, model weights, and model odds were calculated following Anderson (2008).

Results

Population size dynamics

Time series analysis – Figure II-2 shows time series fitted to hybrid and non-recombinant population size data over the 44 week experiment. Hybrid lineages had larger populations than and different population dynamics from non-recombinant populations. The best model for population size dynamics had a main effect of hybrid status and two smoothers: one for hybrid lineages and one for non-recombinant lineages (w = 0.9419, Table II-3). Based on non-overlapping confidence intervals, predicted population sizes of the average hybrid lineage were greater than those of the average non-recombinant lineage after the first eight weeks (Figure II-2). The average hybrid lineage also recovered more rapidly from the population crash most populations experienced around week 16 and plateaued later than the average non-recombinant lineage.

Overall change in population size – At the end of the experiment (week 44), hybrid populations had generally grown more than non-recombinant populations. The GLM model accounting for hybrid status was more strongly supported than the model assuming no difference between hybrid and non-recombinant populations (ΔAICc = 3.34, w = 0.842). Even after model-averaging the parameter estimates, the hybrid lineages were predicted to have 21.48 more individuals than non-recombinant lineages (95% CI = 5.10 – 35.20). Hybrid variance in population growth was 1.88 times greater than that of non-recombinant lineages.

Change in population size by cross type – Table II-6 shows frequencies of additive, dominance, and transgressive patterns by cross type. Hybrid crosses were most frequently found to exhibit evolutionary dominance (18/36), followed by hybrid intermediacy (10/36), and transgressive evolution (8/36; Table II-6; Table II-7). Two thirds (24/36) of the hybrid cross types had at least one ostensibly transgressive population with a growth rate outside the range of all "parental" population. Fifty-five of 160 hybrid line replicates (34.4%) grew faster or slower than their respective "parental" non-recombinant populations.

Change in demographic parameters

Model fitting and parameter estimation – For most cross types (42/48, 87.5%), an LAT model with at least one adaptation parameter was preferred to the model without adaptation parameters (Table II-8). The best model (lowest AICc) was most frequently one with either changing density-dependent effects of larvae on recruitment (Δc_{el}) or changing density-dependent effects of adults on recruitment (Δc_{ea}; Table II-8). ΔAICc scores did not always strongly support a single best model, so parameter estimates were model-averaged for each line (Table II-9). Only one line (BxG) showed no evidence of adaptation (model-averaged estimates $\Delta b = \Delta c_{ea} = \Delta c_{el} = \Delta \mu_l = \Delta \mu_a = 0$; Table II-9).

Hybridization and change in demographic parameters – Hybridization was associated with rapid evolutionary change in the density-dependent effect of larvae on recruitment (Δc_{el}; Table II-10). Δc_{el} was nearly three times larger for hybrid lines than non-recombinant lines ($t_{35} = 2.88$, $p = 0.0067$). Hybrid variance in Δc_{el} was 4.95 times greater than non-recombinant variance.

To illustrate the effects of evolutionary change in demographic parameters, we simulated population dynamics using parameter estimates from one hybrid (DxG) and one non-recombinant (DxD) line with and without adaptation (Figure II-3). To simulate population dynamics without adaptation, we iterated Eqs. 3 and 4 starting with the experimental initial population size of 20 beetles (0 larvae, 20 adults) and substituting the model-averaged parameter estimates for b, c_{ea}, c_{el}, μ_l, μ_a for each line, and no adaptation parameters ($\Delta b = \Delta c_{ea} = \Delta c_{el} = \Delta \mu_l = \Delta \mu_a = 0$). The simulation with adaptation parameters used all ten of the model-averaged parameter estimates for each line (Table II-9). Figure II-3 shows the estimated effects of evolutionary change on population dynamics.

Discussion

Population growth in the challenging new habitat indicates that populations of hybrid origin were generally more successful than the average non-recombinant population. The LAT demographic model shows that this success of hybrid lines is a result of gradual adaptation over 11 generations

rather than initial hybrid vigor simply placing hybrid populations on a more rapid trajectory from the outset (Figure II-3). In most cases (18/36), populations of hybrid origin evolved to resemble the more successful of their parental lines, suggesting that natural selection largely weeded out the traits of one parent in a pattern of evolutionary dominance. However, transgressive evolution was observed in a substantial number of cases (8/36). These cases support the "Evolutionary Novelty" model, in which recombination between distinct lineages produces novel advantageous traits and facilitates evolutionary transitions.

F1 hybrid vigor is frequently observed in many plants, animals and fungi (Rolfe and Hurst 1909; Gray 1954; Shahid et al. 2008), but does not explain our results. In the early generations of the experiment, the average population sizes and estimated demographic parameters were indistinguishable between hybrid and non-recombinant populations. That is, prior to evolutionary change, hybrid populations generally followed the expected pattern, falling midway between their parental lineages. Only after a few generations on soy flour did hybrid populations begin to exhibit superior ecological performance. Fitting the explicit LAT demographic model indicated a three-fold greater rate of evolution per generation in hybrid vs. non-recombinant populations. Thus, hybridization did not instantaneously produce high-performing populations, but rather stimulated a greater rate of evolutionary adaptation on the challenging new medium.

Selective sorting of the recombinant variants in the F2 and later generations can explain rapid evolution in hybrid populations, but does not necessarily result in novelty or enhanced adaptation. For example, in the case of "evolutionary dominance", one parental lineage is unequivocally superior and selection among hybrid genotypes eventually reconstitutes a true-breeding population with the key advantageous traits of that superior parent (Figure II-1B). In this case, hybridization does not generate new advantageous genotypes. The rapid pace of evolution in hybrid populations is caused by elimination of genes from the less well adapted parent, and the outcome is that hybrid populations eventually catch up to the superior parent. Taken on a case-by-case basis, half of our hybrid cross types exhibited final population densities similar to the more successful of their parental lines, consistent with the evolutionary dominance model.

Transgressive evolution results when populations of hybrid origin surpass both parental lineages (Figure II-1C). This pattern is predicted by the "Evolutionary Novelty" model in which certain recombinant genotypes are "hopeful monsters," expressing traits or phenotypic values never seen in either parental population (Dittrich-Reed and Fitzpatrick 2012). If one of these transgressive phenotypes is fortuitously pre-adapted to the novel environment, natural selection can produce a population of true-breeding recombinant genotypes that surpasses anything pre-existing in the parental populations or produced by new mutations in the parental populations. In two thirds of our crosses, at least one replicate population exhibited a pattern of demographic success

consistent with transgressive evolution. This result supports the "Evolutionary Novelty" model and indicates that transgressive evolution can be a frequent outcome of hybridization.

Transgressive evolution is not guaranteed, particularly when severe demographic bottlenecks might allow random fixation of less well-adapted alleles. Almost all of our experimental populations underwent severe bottlenecks in the first few generations of maintenance on soy, creating the opportunity for drift to generate differences among replicates and interfere with efficient selection of the best genotypes. Hybrid populations had greater variation in population growth, based on separate estimates of residual variance for hybrid and non-recombinant populations in the overall population growth analysis. Hybrids also had greater variation in rate of adaptation of the larval density-dependence parameter (Δc_{el}). The greater range of hybrid population performance and adaptation could be the product of the inherent stochasticity of the production of fit hybrid genotypes and/or genetic drift fixing low fitness hybrid genotypes in some populations. If populations of hybrid origin were larger (e.g., initiated with a greater number of founders and/or maintained in larger volumes of flour), or if gene flow among replicates were allowed, we would predict an even more reliable outcome of transgressive evolution.

In our experiment, based on the change in fitted demographic parameters, adaptation predominantly took the form of reduced density dependence. Evolutionary change in population regulation facilitated successful ecological transition to the novel habitat. Egg cannibalism by *T. castaneum* larvae is a common response to suboptimal or challenging diets (Stevens 1989; Via 1999; Agashe et al. 2011). It is possible that the rate of cannibalism (a negative density-dependent effect of larvae on recruitment) was high during the initial transition to soy and subsequently decreased following adaptation of the digestive physiology to soy. Regardless of the mechanism, the observed evolutionary changes affecting population dynamics occurred on approximately the same timescale as population dynamics (Figure II-3), making the interplay of ecological and evolutionary dynamics an exciting aspect of this system.

Historically, many biologists preferred to dichotomize ecological and evolutionary timescales as being so different that one could comfortably study ecology without considering evolution, and vice versa (Slobodkin 1961). This comfortable dichotomy has come under increasing criticism, starting with the first studies of rapid response to selection in the wild (Ford 1964; Endler 1986) and continuing with the development of an entire subdiscipline of eco-evo dynamics (Hairston et al. 2005; Carroll et al. 2007; Schoener 2011). The importance of hybridization has been underappreciated, despite the use of natural hybrid zones in several foundational eco-evo studies (Whitham et al. 2006). Our results demonstrate that hybridization can be a crucial factor affecting the speed and magnitude of evolutionary change, and therefore the tempo and outcome of eco-evo dynamics.

We provide evidence in this article of rapid adaptation to a harsh novel environment and population growth being facilitated by hybridization. Transgressive evolution during hybridization has the potential to elicit rapid population growth and adaptation to a novel environment. These results support the generality of the "Evolutionary Novelty" model of hybridization and the importance of hybridization in the interplay between ecology and evolution in nature.

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Appendix II. Figures and Tables

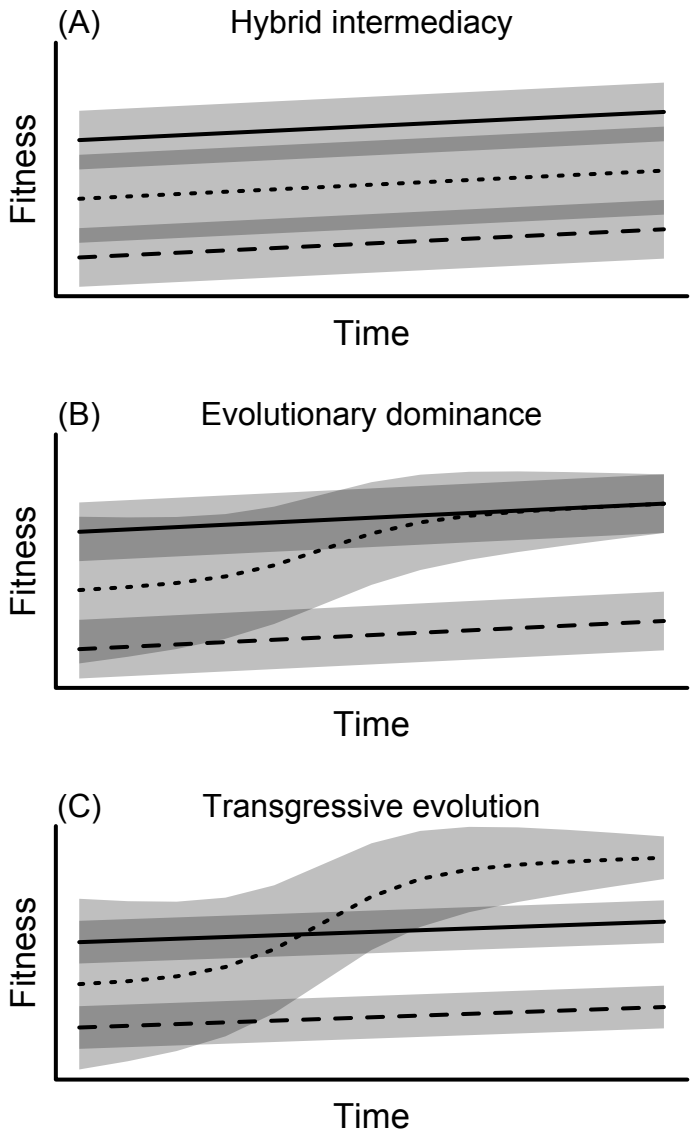

Figure II-1. Hypothetical expectations for changes in mean population fitness during adaptation to a novel environment for two parental populations and a hybrid population composed of offspring from matings between the two parental populations. In all scenarios, parental population 1 (solid line) has higher fitness than parental population 2 (long-dashed line) and the hybrid population (short-dashed line) has intermediate fitness, although initial hybrid mean fitness could be much lower. Shaded regions represent variation in fitness within a population. (A) The naïve expectation that recombination in the early generations of a hybrid population produces phenotypes with intermediate fitness, and that mean fitness will increase at a common rate in all three populations. (B) An alternative expectation in which recombination in the early generations of a hybrid population produces phenotypes with fitness equivalent to parental phenotypes. Thus, hybrid mean fitness increases to the level of the superior parental population as high fitness parental genotypes fix in the hybrid population. (C) An alternative expectation in which recombination in the early generations of a hybrid population results in phenotypes with transgressive fitness. Thus hybrid mean fitness increases beyond the range of the superior parental population as high fitness recombinant genotypes fix in the hybrid population.

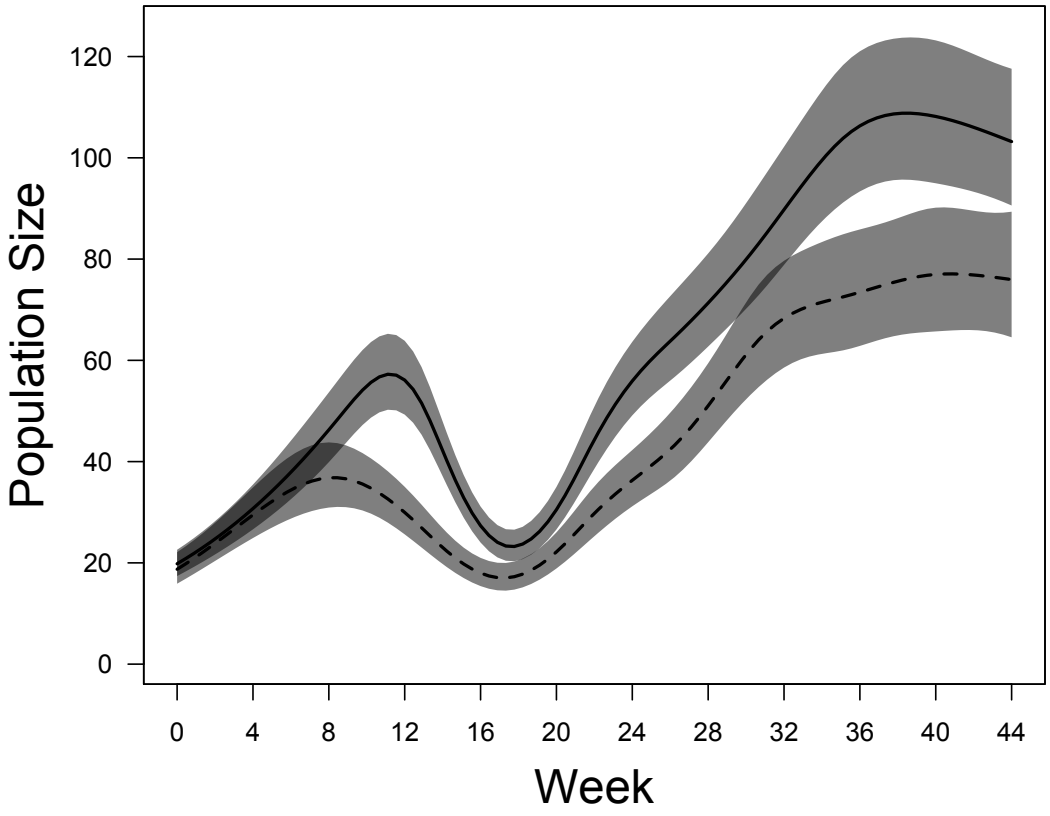

Figure II-2. Fitted population growth over the 44 week experiment for the average hybrid (solid line) and non-recombinant (dashed line) populations. Lines are cubic regression smoothers for fitted population size and shaded regions are 95% confidence intervals. Based on the overlap of confidence intervals, hybrid and non-recombinant populations had equivalent population size through week 8. After week 8 hybrid populations were larger and grew more rapidly than non-recombinant populations.

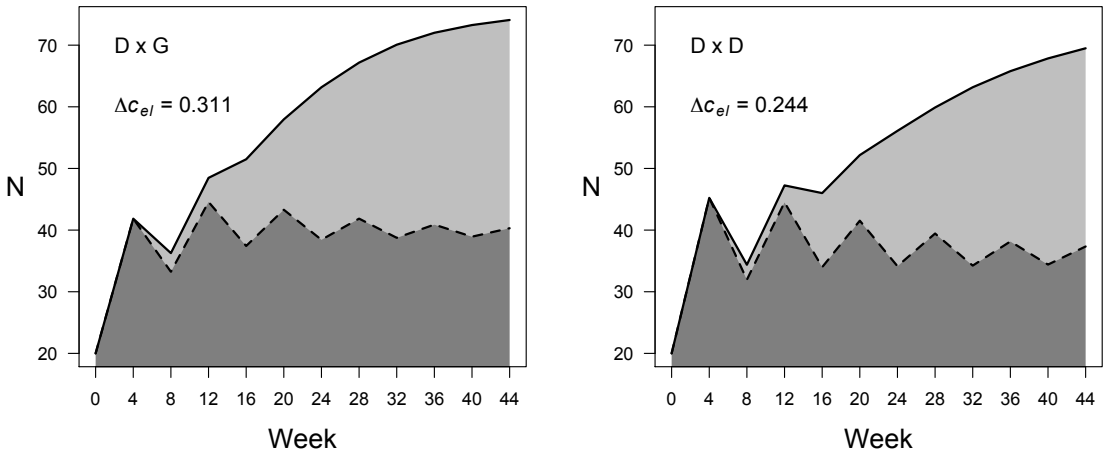

Figure II-3. Simulated population growth over 44 weeks with and without adaptation rate parameters for hybrid cross "DxG" and one of its "parental" types "DxD." Population size was simulated iterating the LAT model (Eqs. 3 and 4) for 11 generations using model-averaged parameter estimates for both cross types. The solid line shows simulations using all ten model-averaged parameter estimates, while the dashed line shows the same simulation without adaptation rate parameters (i.e., $\Delta b = \Delta c_{ea} = \Delta c_{el} = \Delta \mu_l = \Delta \mu_a = 0$). Areas under the lines are shaded to highlight differences in population size between the two simulation conditions for a cross type. Simulations that included adaptation rate parameters almost always produced more rapid population growth and higher final population size than simulations without adaptation rate parameters. "DxG" has a greater value for Δc_{el} than "DxD" and subsequently greater final population size and more rapid population growth.

Table II-1. Original collection localities for source populations.

Collection locality	Year	Grain	ID
India	1989	Rice	A
Royse City, TX, USA	2009	Wheat	B
Bhopal India	2002	Unknown	C
Bellevue, TX, USA	2009	Maize	D
India	1989	Wheat	E
Beaumont, TX, USA	2009	Rice	F
Dar es Salaam, Tanzania	2002	Unknown	G
Japan	1989	Rice	H
Colombia	1989	Maize	I
Murfreesboro, TN, USA	2010	Wheat	J
Japan	1989	Wheat	K
Singapore	1989	Rice	L

Table II-2. Experimental cross design. A-L are source population identification letters (Table II-1). For each cross type, the maternal contributor is labeled first (e.g., cross type "AxB" was founded by "A" females and "B" males). Five replicate populations were founded for each cross type, the number surviving after 44 weeks is in parentheses.

	A	B	C	D	E	F	G	H	I	J	K	L
A	AxA (4)	AxB (5)		AxD (5)		AxF (5)						
B		BxB (4)	BxC (5)		BxE (3)		BxG (4)					
C			CxC (4)	CxD (5)		CxF (5)		CxH (5)				
D				DxD (5)	DxE (5)		DxG (5)		DxI (5)			
E					ExE (5)	ExF (5)		ExH (5)		ExJ (5)		
F						FxF (5)	FxG (5)		FxI (5)		FxK (5)	
G							GxG (5)	GxH (5)		GxJ (5)		GxL (4)
H	HxA (4)							HxH (3)	HxI (5)		HxK (5)	
I		IxB (5)							IxI (4)	IxJ (4)		IxL (3)
J	JxA (5)		JxC (4)							JxJ (4)	JxK (4)	
K		KxB (4)		KxD (5)							KxK (4)	KxL (3)
L	LxA (2)		LxC (3)		LxE (3)							LxL (1)

Table II-3. Model selection to determine whether hybridization affects change in population size. Model degrees of freedom, AICc scores, ΔAICc scores, and model weight (*w*) show that the full model was the best fitting model.

Abbreviated model[1]	Smoother[2]	DF	AICc	ΔAICc	w[3]
$\boldsymbol{y_{ijks} = \alpha + \beta\ \text{Hybrid}_j + f_h(\text{Census}_s)}$	**2**	**12**	**2382.91**	**0.00**	**0.9419**
$y_{ijks} = \alpha + \beta\ \text{Hybrid}_j + f\ (\text{Census}_s)$	1	10	2389.83	6.92	0.0296
$y_{ijks} = \alpha + f_h(\text{Census}_s)$	2	11	2390.00	7.09	0.0272
$y_{ijks} = \alpha + f\ (\text{Census}_s)$	1	9	2396.03	13.12	0.0013

[1]Model parameterizations are the same as for Eq. 1, above. All models also included random intercepts for paternal line a_k, cross type a_{jk}, replicate a_{ijk}, and error term ε_{ijks} (two smoothers) or ε_{ijk} (one smoother). All models also had the same residual variance and correlation structure as in Eq. 1, above.

[2]Models with two smoothers fit smoothing functions to hybrid and non-recombinant time series separately, while models with one smoother fit a single smoothing function to all time series.

[3]Model weight, *w*, is equivalent to a Bayesian posterior probability dependent on the model set.

Table II-4. Models used to identify the best evolutionary hypothesis for each hybrid cross. Each model provides support for one or more evolutionary hypotheses. For each case study only data for a single hybrid cross type *k* and its two corresponding "parental" non-recombinant cross types were included. Binary values are coefficients for the linear combination of model weights of the six models for each evolutionary hypothesis. The hypothesis with the greatest combined model weight is considered to be the best interpretation for a case study.

Model	Formula[1]	Add[2]	IPD[3]	PD[4]	IMD[5]	MD[6]	Trans[7]
1	$\Delta N_{ijk} \sim \alpha_k$	1	0	0	0	0	0
2	$\Delta N_{ijk} \sim \alpha_k + \beta_1 A_{jk}$	1	1	0	1	0	0
3	$\Delta N_{ijk} \sim \alpha_k + \beta_2 M_{jk}$	0	0	0	1	1	0
4	$\Delta N_{ijk} \sim \alpha_k + \beta_3 P_{jk}$	0	1	1	0	0	0
5	$\Delta N_{ijk} \sim \alpha_k + \beta_1 A_{jk} + \beta_4 H_{jk}$	0	0	1	0	1	1
6	$\Delta N_{ijk} \sim \alpha_k + \beta_4 H_{jk}$	0	0	0	0	0	1

[1] ΔN_{ijk} is the change in population size for replicate *i*, cross type *j* (*j* = maternal, hybrid, or paternal), and case study *k* (*k* = 1, 2, …, 36). α_k is the intercept for case study *k*. A_{jk}, M_{jk}, P_{jk}, and H_{jk} are indicator variables for the effects of cross type *j*. Values for maternal, hybrid, and paternal cross types: 2, 1, and 0 for A_{jk}; 1, 1, and 0 for M_{jk}; 0, 1, and 1 for P_{jk}; and 0, 1, and 0 for H_{jk}. $\beta_{1\text{-}4}$ are coefficients for the indicator values for each cross type *j*.
[2] Hybrid intermediacy (Figure II-1A).
[3] Incomplete paternal dominance (Figure II-1B).
[4] Paternal dominance (Figure II-1B).
[5] Incomplete maternal dominance (Figure II-1B).
[6] Maternal dominance (Figure II-1B).
[7] Transgressive Evolution (Figure II-1C).

Table II-5. Population dynamic models with and without adaptation parameters. Values of zero indicate that the adaptation parameter was not included in the model (Eqs. 3 & 4). If the adaptation parameter was "estimated" it was included in the model and estimated by conditional least squares. The nine population dynamic models were fit for each cross type by pooling the time series data for all non-extinct replicate populations.

Model	Δb	$\Delta\mu_l$	$\Delta\mu_a$	Δc_{el}	Δc_{ea}
1	0	0	0	0	0
2	estimated	0	0	0	0
3	0	estimated	0	0	0
4	0	0	estimated	0	0
5	0	0	0	estimated	0
6	0	0	0	0	estimated
7	estimated	estimated	estimated	0	0
8	estimated	estimated	0	0	estimated
9	estimated	estimated	estimated	estimated	estimated

Table II-6. Counts of case studies that support each evolutionary hypothesis based on comparisons of population growth between hybrid crosses and their "parental" non-recombinant cross types. Case studies supported the evolutionary hypothesis with the greatest combined model weight (see Table II-4 for model combinations).

Pattern	Count
Intermediate	**10**
Dominance	**18 (total)**
Maternal	
Incomplete	7
Complete	2
Paternal	
Incomplete	7
Complete	2
Transgressive	**8**

Table II-7. Combined model weights for hybrid case studies.

Hybrid	Trans	Pat	InPat	Mat	InMat	Inter	Pos Trans[1]	Neg Trans[2]	Inter[3]	Total[4]	Interpretation[5]
AxB	0.1501	0.1771	0.2696	0.1073	0.1998	**0.6045**	4	1	0	5	Trans
AxD	**0.8698**	0.1309	0.0399	0.1316	0.0406	0.0732	3	0	2	5	Trans
AxF	0.0929	0.2926	**0.8059**	0.1635	0.6768	0.6268	0	0	5	5	InPat
BxC	0.1484	0.1203	0.2014	0.1205	0.2016	**0.6412**	0	1	4	5	InterW
BxE	0.1754	0.1021	0.1594	0.5769	**0.6342**	0.2808	2	0	1	3	InMat
BxG	0.2806	0.1353	0.1839	0.1253	0.1739	**0.5171**	0	1	3	4	Inter
CxD	0.1017	0.1568	0.3544	0.2441	0.4417	**0.5621**	1	1	3	5	Inter
CxF	0.0902	0.1528	0.4370	0.3545	**0.6388**	0.5055	0	1	4	5	InMat
CxH	0.0885	0.0885	0.0190	**0.9797**	0.9101	0.0195	0	0	5	5	Mat
DxE	0.1024	0.1886	0.3854	0.2155	0.4123	**0.5625**	0	1	4	5	Inter
DxG	0.2265	0.1181	0.1865	0.2884	0.3567	**0.4603**	0	3	2	5	Inter
DxI	0.1065	0.1094	0.2066	0.7024	**0.7996**	0.2462	2	0	3	5	InMat
ExF	0.1389	**0.9987**	0.8611	0.1389	0.0013	0.0013	0	0	5	5	Pat
ExH	0.4262	0.4066	0.0059	**0.9683**	0.5676	0.0102	3	0	2	5	Mat
ExJ	0.1272	0.1220	0.2320	0.1766	0.2865	**0.6156**	1	0	4	5	Inter
FxG	0.1143	0.6115	**0.8555**	0.1300	0.3740	0.3661	0	1	4	5	InPat
FxI	0.2162	0.2189	0.5427	0.4568	**0.7806**	0.5403	0	0	5	5	InMat
FxK	0.1020	0.1102	0.2147	0.7496	**0.8541**	0.2246	0	0	5	5	InMat
GxH	0.1052	0.1275	0.4470	0.5294	**0.8489**	0.4407	0	0	5	5	InMat
GxJ	0.0979	0.6010	**0.8031**	0.1111	0.3131	0.3411	0	1	4	5	InPat
GxL	0.0560	0.0894	0.3017	0.5131	**0.7254**	0.4145	0	0	4	4	InMat
HxA	0.2020	**0.9548**	0.7846	0.1845	0.0144	0.0241	2	0	2	4	Pat
HxI	**0.5241**	0.4489	0.3401	0.1598	0.0510	0.1475	4	0	1	5	Trans
HxK	**0.9162**	0.1692	0.0443	0.1388	0.0140	0.0364	5	0	0	5	Trans
IxB	0.1105	0.8232	**0.8812**	0.1129	0.1708	0.1713	0	0	5	5	InPat
IxJ	0.3000	0.2929	0.3297	0.0962	0.1330	**0.4012**	0	0	4	4	Inter
IxL	**0.8061**	0.0501	0.0522	0.0207	0.0229	0.1398	3	0	0	3	Trans

Table II-7. Continued.

Hybrid	Trans	Pat	InPat	Mat	InMat	Inter	Pos Trans[1]	Neg Trans[2]	Inter[3]	Total[4]	Interpretation[5]
JxA	0.1053	0.2529	0.4191	0.1269	0.2931	**0.5688**	0	0	5	5	Inter
JxC	0.0825	0.8749	**0.9075**	0.0843	0.1169	0.1188	0	0	4	4	InPat
JxK	0.1049	0.1119	0.2044	0.1084	0.2009	**0.6942**	0	0	4	4	Inter
KxB	0.1324	0.3822	**0.5023**	0.0962	0.2163	0.4584	2	0	2	4	InPat
KxD	0.1822	0.3104	0.3937	0.1123	0.1955	**0.4779**	3	0	2	5	Inter
KxL	0.3365	0.0935	0.1283	0.0417	0.0765	**0.5346**	3	0	0	3	Trans
LxA	0.2579	0.1370	0.1532	0.0229	0.0392	**0.5885**	2	0	0	2	Trans
LxC	0.0381	0.7326	**0.7528**	0.0237	0.0439	0.2278	1	0	2	3	InPat
LxE	**0.8053**	0.1773	0.0619	0.1468	0.0314	0.1216	3	0	0	3	Trans

[1]The number of replicates with greater change in population size than either parental type.

[2]The number of replicates with less change in population size than either parental type.

[3]The number of replicates with change in population size within the range of both parental types.

[4]The total number of replicates per hybrid type surviving after 44 weeks.

[5]Final interpretation might differ from best interpretation if all replicates are outside the range of both parental types. Interpretations are the same as in Table II-6.

Table II-8. AICc scores by cross type. Model numbers the same as in Table II-5. The model with lowest AICc is in bold.

Cross	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7	Model 8	Model 9
AxA	221.36	**220.15**	224.14	224.29	224.14	222.64	226.25	227.25	234.21
AxB	820.71	816.12	823.30	823.30	**815.48**	816.50	822.62	828.82	833.83
AxD	309.82	**304.18**	312.41	309.70	312.41	304.67	309.16	306.48	312.61
AxF	266.99	268.02	269.58	268.79	**252.64**	255.48	273.38	261.04	258.19
BxB	184.27	199.22	187.05	183.64	**177.17**	185.48	190.73	191.58	189.83
BxC	266.60	268.81	269.19	269.19	269.19	**264.16**	274.37	269.71	275.84
BxE	161.73	148.79	165.24	150.10	**132.17**	144.94	157.63	154.08	145.04
BxG	**645.78***	648.56*	648.56*	648.56*	648.56*	648.56*	650.28*	646.83	651.70
CxC	229.83	221.64	232.61	231.37	227.25	**211.82**	227.74	217.92	220.33
CxD	843.19	803.36	845.38	844.84	**769.21**	773.16	804.91*	792.27*	798.40*
CxF	269.32	272.11	271.91	271.91	271.91	**266.91**	277.66	272.47	270.02
CxH	293.49	287.48	296.59	284.84	**258.59**	295.01	290.38	285.55	272.42
DxD	289.26	280.51	291.92	279.68	**268.84**	284.82	280.71	286.10	280.44
DxE	260.93	252.89	263.52	254.67	**229.30**	260.46	258.44	255.65	241.47
DxG	281.61	277.57	284.20	278.99	**257.19**	279.78	281.72	284.70	266.06
DxI	330.35	327.62	332.94	329.05	**311.45**	328.14	332.66	334.14	317.37
ExE	227.35	234.96	225.56	**223.61**	232.77	234.60	236.52	236.42	248.05*
ExF	264.51	264.89	267.10	261.91	267.10	258.95	265.89	267.40	**243.15**
ExH	303.81	303.58	307.83	299.86	**284.13**	305.35*	305.76	309.00	299.01
ExJ	285.27	263.69	287.86	280.86	**247.46**	265.01	269.25	269.56	252.21
FxF	211.29	221.49	213.87	213.88	208.89	**203.98**	220.59	209.53	215.66
FxG	260.20	262.84	262.79	262.79	256.54	**256.34**	268.40	261.91	268.02
FxI	353.34	353.33	355.92	**350.92**	355.93	352.36	357.82	357.90	358.76
FxK	290.75	281.07	293.34	274.86	**246.79**	289.30	279.49	274.53	257.30
GxG	**816.65***	819.29*	819.24*	819.24*	819.01*	990.55	903.34*	903.93*	910.52*
GxH	828.36*	830.94*	830.95*	830.95*	826.19*	**801.81**	823.29*	827.10*	833.23*
GxJ	257.37	254.66	259.96	258.71	**246.83**	253.21	260.16	258.71	257.30

Table II-8. Continued.

Cross	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7	Model 8	Model 9
GxL	643.45*	646.24*	646.23*	646.23*	640.52*	**607.07**	636.61*	640.48*	647.43*
HxH	**559.59***	562.79*	562.75*	562.75*	563.41*	563.48*	567.39*	571.32*	580.04*
HxI	1307.50*	1309.75*	1310.09*	1310.10*	**1304.12***	1309.35*	1315.34*	1317.66*	1323.79*
HxK	337.33	304.32	339.93	328.65	339.92	316.09	309.59	310.02	**291.66**
HxA	225.87	228.52	228.96	225.28	228.65	**224.53**	234.53	230.59	229.04
IxI	**1122.67***	1125.45*	1125.45*	1125.45*	1125.33*	1123.05*	1128.55*	1132.04*	1138.98*
IxJ	685.93*	685.77*	688.71*	688.71*	688.70*	**664.49**	697.68*	691.98*	698.92*
IxL	187.08	178.53	188.55	178.66	**167.00**	175.94	184.26	183.02	178.41
IxB	807.92*	810.45*	810.51*	810.51*	810.46*	**761.64**	874.44*	811.70*	818.70*
JxJ	205.51	213.46	208.27	**188.76**	196.28	218.86	205.25	218.07	209.32
JxK	**641.28***	644.06*	644.06*	644.06*	645.72*	645.76*	650.18*	650.73*	650.73*
JxA	200.89	194.02	204.22	203.58	195.84	**189.62**	200.30	194.61	191.79
JxC	168.06	162.44	170.84	170.69	**154.63**	166.55	168.64	168.70	163.23
KxK	728.22*	730.99*	731.00*	731.00*	730.98*	**719.31***	756.02	761.01	809.47*
KxL	167.25	**149.55**	161.28	155.30	170.92	153.21	152.84	153.09	158.20
KxB	636.46*	639.22*	639.24*	639.24*	700.49	**596.27**	719.55*	647.88*	654.82*
KxD	**792.96***	795.55*	795.55*	795.55*	794.50*	795.69*	810.59*	800.59*	806.72*
LxL	323.60*	338.40*	338.60*	338.60*	338.60*	338.43*	458.60*	458.44*	**98.39***
LxA	128.16	113.50	128.86	**96.98**	110.41	100.33	104.09	110.80	125.68
LxC	480.22*	483.31*	483.37*	483.37*	483.39*	**447.73**	533.11*	489.28*	498.01*
LxE	515.01*	515.37*	518.16*	518.16*	518.18*	**491.25**	541.60	523.32*	532.04*
Sum	6	3	0	4	17	15	0	0	3

*Models for which tolerance was relaxed in order for the *optim* function to reach convergence.

Table II-9. Model-averaged parameter estimates. BM is the model with lowest AICc, the "best model."

Cross	BM	*b*	*Δb*	*cea*	*Δcea*	*cel*	*Δcel*	*mul*	*Δmul*	*mua*	*Δmua*
AxA	2	0.94167	0.09529	0.0242	0.02814	0.00418	0.00101	0.28681	0	0.39576	0.00249
AxB	5	0.14539	0	0.08815	0.00237	0.26618	0.01417	0.74633	0.00137	0.05874	0.00537
AxD	2	1.44736	0.11973	0.02734	0.03151	0.00022	0.00017	0.30734	0.00059	0.34158	0.0021
AxF	5	3.04669	0.00001	0.01856	0.02003	0.0203	0.19537	0.04091	0.00001	0.56085	0
BxB	5	2.86389	0.00007	0.02399	0.00124	0.02503	0.20149	0.22827	0.00127	0.48073	0.00186
BxC	6	1.83479	0.00153	0.02624	0.03009	0	0.00207	0	0	0.55215	0
BxE	5	1.70266	0.00007	0.01347	0.0005	0.07727	0.34253	0.74551	0.00008	0.04214	0.00006
BxG	1	1.13577	0	0.06641	0	0	0	0.10047	0	0.1005	0
CxC	6	5.04802	0.00127	0.06783	0.08482	0.00956	0.0013	0	0.00257	0.56892	0.00049
CxD	5	2.58244	0	0.88527	0.11173	2.27496	0.60082	0.15434	0.00006	0.16363	0
CxF	6	1.89507	0.00046	0.02126	0.04259	0.00473	0.02266	0.00917	0	0.46808	0
CxH	5	2.51166	0.00006	0.01853	0	0.05735	0.28467	0.59243	0	0.2059	0
DxD	5	4.19785	0.00069	0.04206	0.00369	0.04831	0.2436	0.35451	0	0.54863	0.00325
DxE	5	2.89552	0	0.03375	0.00012	0.05393	0.25572	0.40881	0	0.34525	0.00001
DxG	5	3.10538	0.00001	0.03392	0.00058	0.04566	0.31078	0.28492	0	0.4832	0
DxI	5	2.36501	0.00008	0.02907	0.00447	0.05768	0.31821	0.1539	0.00001	0.54751	0.00001
ExE	4	4.02623	0.00034	0.02599	0.00016	0.02161	0.00063	0.73338	0.00976	0.42473	0.06084
ExF	9	4.34007	0.00001	0.03268	0.07186	0.03308	0.21019	0.26572	0	0.41039	0.01808
ExH	5	4.39417	0.00004	0.0307	0	0.03429	0.21372	0.51698	0	0.44579	0.00003
ExJ	5	2.61074	0.00008	0.03647	0.00631	0.06898	0.31436	0.45266	0	0.32792	0
FxF	6	3.52972	0.00002	0.02578	0.07672	0.00818	0.00782	0.17184	0	0.41199	0
FxG	6	3.10229	0.00014	0.02129	0.03752	0.01183	0.05859	0.03796	0	0.59855	0
FxI	4	3.18362	0.0096	0.02613	0.01024	0	0.00087	0.06877	0.00028	0.79092	0.03143
FxK	5	3.40462	0	0.01779	0.00026	0.04559	0.29413	0.51398	0	0.29732	0
GxG	1	0.9849	0.00169	0.28354	0	0	0.00526	0.10078	0	0.10733	0
GxH	6	1.22206	0.00019	7.3758	0.93882	0.00694	0.00135	0.73814	0.00804	0.02734	0

Table II-9. Continued.

Cross	BM	*b*	*Δb*	*cea*	*Δcea*	*cel*	*Δcel*	*mul*	*Δmul*	*mua*	*Δmua*
GxJ	5	3.76372	0.00155	0.04623	0.00217	0.03258	0.14461	0.09788	0	0.56818	0.00008
GxL	6	1.0938	0	9.4549	0.94786	0.0097	0.00098	0.6674	0.00012	0.05611	0
HxA	6	2.46906	0.01363	0.03033	0.05975	0.00627	0.00672	0.10896	0.01467	0.66072	0.01353
HxH	1	0.91094	0	0.6237	0.01967	0.5967	0.0153	0.10077	0	0.12999	0
HxI	5	1.32599	0.1364	0.3343	0.02183	6.68667	0.2161	0.79878	0.00002	0.99158	0
HxK	9	5.67795	0.06353	0.06834	0.12242	0.07054	0.23404	0.48099	0.00001	0.28236	0
IxB	6	1.82162	0	8.40616	0.93373	0.01162	0.00022	0.68501	0.00487	0.14021	0
IxI	1	0.6221	0.01312	2.7045	0.28631	0.35361	0.0243	0.10316	0	0.01852	0
IxJ	6	1.9648	0.0011	9.4899	0.93383	0.01495	0.00085	0.68826	0	0.05467	0
IxL	5	2.77143	0.0014	0.01882	0.00278	0.06177	0.26465	0.72467	0.00007	0.22801	0.00134
JxA	6	2.26737	0.01003	0.05029	0.11612	0.01527	0.04602	0.05259	0.00192	0.61927	0
JxC	5	1.77517	0.00441	0.02244	0.00131	0.03898	0.24918	0.29949	0	0.27455	0.00063
JxJ	4	2.6584	0.00004	0.04549	0	0.00115	0.00788	0.23468	0.00001	0.8775	0.06894
JxK	1	0.86045	0	0.04868	0.01311	0.46392	0.0061	0.10241	0	0.10108	0
KxB	6	1.70868	0	9.5357	0.99621	0.0111	0.00135	0.715	0.00085	0.06155	0
KxD	1	0.94787	0	0.00837	0.00493	0.12789	0	0.10108	0	0.10049	0
KxK	6	0.01731	0.00031	17.07675	0.97816	0.46677	0.00163	0.1064	0	0	0
KxL	2	0.61951	0.3636	0.03021	0.05849	0.01322	0.00195	0.43965	0.0247	0.39842	0.00942
LxA	4	1.67864	0.00293	0.04709	0.04801	0.00619	0.00039	0.46576	0.00003	0.85437	0.25318
LxC	6	1.35671	0	12.12761	1	0.01708	0.00029	0.66595	0	0.01288	0
LxE	6	2.49336	0.00005	18.20263	0.95776	0.02217	0.00003	0.49097	0.00005	0.34422	0
LxL	9	0.99394	0.07089	0.49172	0.42326	0	0.00588	0.19207	0	0.99877	0

Table II-10. Estimates of the effect of hybrid status on adaptation parameters with standard errors. The estimates are means of model-averaged parameter estimates for hybrid and non-recombinant parental types (after correcting for shared ancestry and unequal variance, see Eq. 5). On average, hybrids had greater Δc_{el} than non-recombinants.

Parameter	Hybrid status	Est.	S.E.	t_{35}	p
Δb	Hybrid	0.0203	0.0111	1.8227	0.0769
	Non-recombinant	0.0153	0.0144	-0.3459	0.7315
Δc_{el}	**Hybrid**	**0.1282**	**0.0287**	**4.4626**	**0.0001**
	Non-recombinant	**0.0430**	**0.0296**	**-2.8814**	**0.0067**
Δc_{ea}	Hybrid	0.2091	0.0781	2.6767	0.0112
	Non-recombinant	0.1585	0.0825	-0.6135	0.5435
$\Delta \mu_l$	Hybrid	0.0016	0.0008	1.9796	0.0557
	Non-recombinant	0.0011	0.0012	-0.4081	0.6857
$\Delta \mu_a$	Hybrid	0.0093	0.0070	1.3213	0.1950
	Non-recombinant	0.0115	0.0101	0.2154	0.8307

Chapter 3. Hybridization and life history evolution during an ecological transition

Abstract

Gaining a deeper understanding of the processes driving adaptation to new resources is paramount for evolutionary biology. Rates of evolution for adaptive traits depend on genetic variances and covariances, and therefore, might be changed dramatically by the process of hybridization. Hybridization between genetically distinct populations can constrain or enhance the origin and spread of adaptations. The predictability of these alternative outcomes is largely unknown. Previously, we found that hybridization consistently enhanced population-level performance in a challenging new environment in an experiment using 36 different hybrid crosses among 12 distinct lineages of the red flour beetle (*Tribolium castaneum*; see Chapter 2). In particular, there was often a pattern of "transgressive evolution" in which populations of hybrid origin ultimately gave rise to descendants with higher mean population fitness in the new environment than those descended from either non-recombinant parental line. Here we test whether adaptation to the novel environment (soy medium) was associated with evolutionary change in developmental rates underlying timing and size at metamorphosis. Over 11 generations of selection in soy flour, the developmental rates of hybrid lines increased significantly while non-recombinant lines' developmental rates increased only slightly, supporting a pattern of transgressive evolution of development. Evolution of accelerated developmental rate was not correlated with previously observed evolution of decreased larval density dependence (see Chapter 2). During the ecological transition to soy, hybridization facilitated adaptation along multiple dimensions, manifested separately at the population and individual levels.

Introduction

Historically, hybridization was generally viewed as an evolutionary dead-end or the final stage of speciation, resulting in inviable or infertile offspring with little evolutionary potential (Dobzhansky 1936, 1937; Mayr 1942; Coyne and Orr 2004). In contrast, the Evolutionary Novelty hypothesis predicts that the increase in genetic variation and subsequent increase in phenotypic variation could produce a few recombinant genotypes with higher fitness compared to parental genotypes, at least in some environments (Anderson and Stebbins 1954; Arnold 1997). These hopeful recombinants might become established as evolutionarily independent lineages with novel ecological characteristics (Dittrich-Reed and Fitzpatrick 2012), a phenomenon we have called transgressive evolution (see Chapter 2) to distinguish the evolutionary outcome from transgressive segregation (the occurrence of hybrids with exceptional phenotypes in the F2 generation (Rieseberg et al. 1999)) or "evolutionary dominance", in which the outcome of selection on a hybrid population is the recovery of one (presumably better adapted) parental phenotype (see Chapter 2).

The conceptual model of evolutionary novelty arising from hybridization is supported by computer simulations (Buerkle et al. 2000; Barton 2001; Duenez-Gusman et al. 2009) and some case studies (Rieseberg et al. 2003; Schwarz et al. 2005; Gompert et al. 2006; Mavarez et al. 2006; Agashe et al. 2011). However, the importance of hybridization in adaptation to novel environments is contested (see: Arnold 1997; Coyne and Orr 2004; Arnold 2006) because we do not know whether hybridization regularly enhances the probability of ecological speciation. Here we take an experimental approach to evaluate whether hybridization frequently promotes rapid adaptation to a challenging new habitat via increased developmental rate.

In this study we use developmental rate as a measure of performance in a novel environment. Tribolium, like many insects, respond to plastically stress (*e.g.,* a harsh novel diet) by increasing the number of larval instars and decreasing the overall larval developmental rate (Mikel and Standish 1947; Sokoloff et al. 1966; Via and Conner 1995). There is genetic variation in the degree of depression of developmental rate in a stressful environment and, consequently, developmental rate is subject to selection (Bergerson and Wool 1986; Bergerson and Wool 1988; Via 1991; Via and Conner 1995). For holometabolous insects with short generation times, developmental rate is an important component of lifetime fitness. Faster developmental rates allow for earlier reproduction, higher per capita birth rates and subsequently greater intrinsic growth rates (Arendt 1997). However, there can be a trade-off between rapid developmental rate and survival to maturity or developmental rate and adult size (Sevenster and Vanalphen 1993; Chippindale et al. 1997). The evolution of accelerated developmental rate in a novel environment coupled with a loss of performance in the ancestral environment (not necessarily due to a trade-off) could promote diversification through ecological speciation (Schluter 2001).

In this article, we ask whether hybrid populations of *T. castaneum* evolved faster larval developmental rates relative to non-recombinant populations, demonstrating more rapid adaptation to a stressful novel medium. To answer this question we assayed developmental rate for 12 distinct non-recombinant lines and 36 hybrid lines every four weeks, beginning on the eight week, for 44 weeks (~11 generations). Previous results from these experimental populations demonstrated population-level adaptation in the form of increased demographic rates by the end of the 44 weeks (see Chapter 2). Hybrid populations tended to evolve more rapidly, with some clearly outperforming their parental lineages. A model-based analysis indicated that high-performing populations had evolved less severe density-dependent feedbacks of adults and larvae on recruitment. Here we investigate the evolution of individual performance in hybrid vs. non-recombinant populations while controlling for population ecology, and then ask whether individual level and population level measures of performance are correlated. We tested whether hybrid populations adapted to the new medium more rapidly than non-recombinant populations by comparing developmental rates using statistical models that accounted for non-independence between and within populations. Our data demonstrate that hybrid lines typically evolved faster

developmental times than non-recombinant lines – a consistent signal of transgressive life-history evolution. The magnitude of developmental rate evolution was not correlated with change in population level demographic rates, suggesting that they represent distinct dimensions of adaptation. Hybridization tended to enhance adaptation at both population and individual levels, but the signal was more consistent for the individual-level developmental rates.

Methods

Model system

Tribolium castaneum (Coleoptera, Tenebrionidae), red flour beetles, are ideal models for testing hypotheses about developmental evolution during adaptation. *T. castaneum* are simple to maintain, have a relatively simple ecology, and short generation time (Sokoloff 1972). Moreover, unfavorable diets increase larval developmental time and subsequently decrease adult fecundity (Sokoloff et al. 1966; Bergerson and Wool 1988; Via 1991, 1999; Fardisi et al. 2013). There is genetic variation within and between populations in developmental time on different media and developmental time can respond to selection (Sokoloff et al. 1966; Bergerson and Wool 1988; Via 1991, 1999).

T. castaneum are cosmopolitan pests of stored food products, especially in tropical and subtropical latitudes (Sokoloff 1972). The beetles used in this experiment were all originally collected from stored grain, so a container of grain may be considered an excellent natural mesocosm. Whole wheat flour supplemented with brewer's yeast, inactive *Saccharomyces cerevisiae*, is the standard medium for *Tribolium* culture and the "ancestral environment" for this study. Soy flour medium, the "novel environment", increases developmental time and number of larval instars (Mikel and Standish 1947), inhibits protein digestion (Lipke et al. 1954), and decreases productivity (Sokoloff et al. 1966).

Experimental lines

We compared developmental rate of beetles drawn from 180 hybrid and 60 non-recombinant lines undergoing selection in soy medium. The generation of hybrid and non-recombinant populations used in this experiment is described in Chapter 2. Briefly, five replicate lines were founded for each of 12 strains of *T. castaneum* (non-recombinant lines) and 36 crosses between pairs of those 12 strains (hybrid lines). Each of these populations was maintained on soy flour medium (95% soy flour, 5% Brewer's yeast) for 44weeks (~ 11 generations) at 34 C, 45% r.h., and on a 12 hr light cycle. While all 48 cross types are represented by at least one population, due to extinctions and missing data, only data on developmental rates from 207 populations (160 hybrid, 47 non-recombinant) are included in this study.

Larval development assay

Every four weeks, beginning eight weeks after selection on soy medium initiated, we censused each experimental population and recorded the number of larvae, pupae, and adults. During a census, we removed six females from each population and allowed three to oviposit on 1 mL soy medium (ca. 0.4 g) and three to oviposit on 1mL wheat medium (ca. 0.5 g) for 24 hrs before being returned to their populations. After 28 days of incubation at 34 C, 45% r.h., and on a 24 hr dark cycle, we counted living offspring and recorded the developmental stage of each (larva, pupa, or adult). Although it would have been ideal to measure developmental rate directly as the number of days an individual spent in each stage, it was impractical to do so for multiple individuals from 207 populations developing in both wheat and soy media. No females were removed for larval development assays during week 36.

Developmental stage analysis

To determine whether hybridization promoted greater change in larval developmental rate over time, we tested whether changes in the proportions of three developmental stages (larva, pupa, and adult) were best described by the interaction of hybridization, medium, and time, or simpler models with fewer parameters. Since we did not measure developmental rate directly, we fit proportional odds logistic mixed models to numbers of offspring at each developmental stage (larva, pupa, adult) after 28 days incubation. We included random intercepts for maternal strain, paternal strain, and population to account for shared ancestry (non-independence among populations). We also included a parameter representing the demographic conditions in the experimental population being assayed to account for temporal auto-correlation (non-independence within populations, see below).

The full model can be expressed as follows:

$$\text{logit}[\Pr(Y_{ijk} > y_{ijkl})] = \alpha_l + \beta_h h + \beta_t t + \beta_m m + \beta_{ht} ht + \beta_{hm} hm + \beta_{tm} tm + \beta_{htm} htm + \delta_a a + a_i + a_j + a_k + \varepsilon_{ijk}, \quad (6)$$

where y_{ijkl} is the rank (l) of a beetle surviving after 28 days incubation from replicate i, paternal line j, and maternal line k ($y_{ijk1} = 1$ for larvae, $y_{ijk2} = 2$ for pupae, and $y_{ijk3} = 3$ for adults). The fitted parameter α_l describes the odds of a developmental transition after 28 days incubation in soy medium for an average hybrid beetle at the beginning of the experiment. The coefficients β describe changes in developmental rate with hybrid status ($h = 1$ for parental, 0 for hybrid lines), time t, medium ($m = 1$ for wheat, 0 for soy), and their two- and three-way interactions. a_k, a_j, and a_i are random effects of maternal line, paternal line, and replicate, respectively. The effect of demography is described by δ_a, see below. We fit proportional odds logistic regression models with the *clmm* function of the R package *ordinal* (Christensen 2012). We compared models using Akaike's Information Criterion (AIC; Burnham and Anderson 2004).

Our model selection process had two stages. First, we determined the best variable to account for plasticity in developmental rate due to the assayed population's demography. This was motivated by the casual observation that fluctuations in fecundity and developmental rate seemed to follow fluctuations in population density. Negative feedback of population density on individual fecundity has been reported in *Tribolium* and other insects (Peters and Barbosa 1977; Rossiter 1991; Morag et al. 2011), and the effect has the potential to obscure other influences on fecundity and development (Fox et al. 1997). Specifically, we tested whether the population density females experienced as adults (current population census), as larvae (previous census), or the change in population density during development (log transformed ratio of current to previous census) affected developmental rate in the next generation. We measured population density three different ways (as the number of larvae, adults, or both) for a total of nine demographic parameters. To determine which of these nine demographic parameters best explained developmental rate plasticity, we compared AICs of full models that differed only by demographic parameter (Table III-1). Second, including the demographic parameter from the best fitting model in the first step as a fixed effect, we compared the full model to several reduced, biologically interesting models (Table III-2). We calculated model-averaged marginal probabilities of observing larvae, pupae, and adults after 28 days for all fixed effects using the 95% confidence set of models (Anderson 2008). Due to a lack of census data for weeks 4 and 36 (see Chapter 2), data from weeks 8 and 40 were excluded from the analysis.

Developmental rate and larval density dependence

The experimental populations evolved decreased larval density dependence over the duration of the experiment (see Chapter 2). To determine whether the adaptation to soy medium observed at the individual level was related to adaptation at the population level, we tested for a relationship between the change in developmental rate on soy medium and the previously estimated change in larval density dependence (Δc_{el}). Additionally, to determine whether loss of performance on wheat medium at the individual level was related to adaptation to soy medium at the population level, we repeated this test using the change in developmental rate on wheat medium. We approximated developmental rate as the mean rank of the developmental stages of the assay offspring (adults: 3; pupae: 2; larvae: 1). Δc_{el} was estimated for each cross type, therefore developmental rates were averaged across replicate populations for each cross type. We calculated change in developmental rate for each cross type as the log transformed ratio of week 44 to week 12 mean developmental rates. We fit a linear mixed model to the change in larval density dependence. We included random intercepts for maternal strain to account for shared ancestry (non-independence among populations).

The full model is as follows:

$$y_j \sim \alpha + \beta_d \Delta d_j + \beta_h h_j + a_k + \varepsilon_{jk}, \quad (7)$$

where y_j is the change in larval density dependence for cross type j ($\Delta c_{el\,j}$). The fitted parameter α describes the marginal mean Δc_{el} for hybrid cross types. The coefficients β describe changes in Δc_{el} with change in developmental rate (d) or hybrid status (h = 1 for parental crosses, 0 for hybrid crosses). The fitted parameter a_k is the random effect of maternal line. In the first analysis, Δd_j represents change in developmental rate in soy medium. In the second analysis, Δd_j represents change in developmental rate on wheat medium. We fit linear mixed models with the *lme* function of the R package *nlme* (Pinheiro et al. 2012).

Offspring count analysis

As in the developmental stage analysis above, to determine whether hybridization promoted greater change in productivity over time, we tested whether changes in the total number of offspring surviving after 28 days were best described by the interaction of hybridization, environment, and time, or simpler models with fewer parameters (Table III-3). We fit linear mixed models to the log-transformed number of offspring per assay. We included random intercepts for maternal strain, paternal strain, and population to account for shared ancestry (non-independence among populations). We also included the best fitting demographic variable from the first stage of model selection for the developmental stage analysis (see above) to account for temporal auto-correlation (non-independence within populations). The full model can be expressed as follows:

$$y_{ijk} = \alpha + \beta_h h + \beta_t t + \beta_m m + \beta_{ht} ht + \beta_{hm} hm + \beta_{tm} tm + \beta_{htm} htm + \delta_a a + a_i + a_j + a_k + \varepsilon_{ijk}, \quad (8)$$

where y_{ijk} the logarithm of the total number of offspring surviving after 28 days incubation (productivity) for replicate i, paternal line j, maternal line k. The fitted parameter α describes productivity in soy medium for the average hybrid population at the beginning of the experiment. The coefficients β describe changes in productivity with hybrid status (h = 1 for parental, 0 for hybrid lines), time t, medium (m = 1 for wheat, 0 for soy), and their two- and three-way interactions. a_j, a_k, and a_i are random effects of paternal line, maternal line, and replicate, respectively. The effect of demography is described by δ_a, see above. We fit linear mixed models with the *lme* function of the R package *nlme* (Pinheiro et al. 2012). We compared the same set of models as in the second round of model selection for the developmental data using Akaike's Information Criterion (AIC; Burnham and Anderson 2004).

Testing for a trade-off

To evaluate whether performance on soy comes at the expense of performance on wheat, we tested for negative correlations between productivity on soy and wheat and between developmental rate on soy and wheat (Levins 1962). A simple correlation test might miss a genetic trade-off if there is a "silver spoon" effect, a positive phenotypic correlation owing, for example, to maternal size or health (Grafen 1988; Agrawal et al. 2010). Therefore, to provide a more nuanced test for trade-offs, we performed analyses including fixed effects of hybrid status, and change in adult density in the assayed population and random intercepts for maternal strain, paternal strain, and replicate population. In the first analysis, we tested for a trade-off between wheat productivity at week 12 and soy productivity at week 12 (earliest productivity/developmental rate data with demographic data). We repeated this analysis for wheat and soy productivity at week 44 (final census) and for wheat and soy developmental rates at weeks 12 and 44.

The generic model is expressed as follows:

$$y_{ijk} = \alpha + \beta_x x_{ijk} + \beta_h h + \delta_a a + a_i + a_j + a_k + \varepsilon_{ijk}, \quad (9)$$

where y_{ijk} is performance in soy medium and x_{ijk} is performance in wheat medium for replicate i, paternal line j, and maternal line k. We performed four analyses in which performance was defined as early productivity (week 12), late productivity (week 44), early developmental rate, or late developmental rate. The fitted parameter α describes marginal mean performance in soy medium for the average hybrid population. The coefficients β describe the change in soy performance with wheat performance (x) and hybrid status (h = 1 for parental, 0 for hybrid lines). a_j, a_k, and a_i are random effects of paternal line, maternal line, and replicate, respectively. The effect of demography is described by d_a, see above. We fit linear mixed models fit with the *lme* function of the R package *nlme* (Pinheiro et al. 2012).

Results

Developmental stage analysis

The 95% confidence set of models in the first round of model selection included only the model with change in adult population size (ΔAIC = 0.00, w = 0.951; Table III-1). We can infer that females that develop in growing populations produce more rapidly developing offspring. This parameter (ΔA) was used as the maternal demographic parameter (a) in the second round of model selection, and subsequent analyses of developmental rate and productivity. Most populations fluctuated, so the rate and direction of change was not confounded with time.

The 95% confidence set of models in the second round of model selection included the full model (ΔAIC = 1.222, w = 0.341; Table III-2) and the model with all two-way interactions (ΔAIC = 0.00, w = 0.628; Table III-2). The developmental rate of hybrid lines on soy medium increased more rapidly than that of non-recombinant lines (Figure III-1; Table III-4). The developmental rate of hybrid lines on wheat decreased more slowly than that of non-recombinant lines (Figure III-1; Table III-4). The evolution of accelerated developmental rate in soy medium is unlikely to be correlated with smaller adult size at eclosion because we did not observe a correlation between adult size and time or population density (see Chapter 2). Taken together, hybrid ancestry was associated with the evolution of faster development in the novel medium, and non-hybrid ancestry was associated with evolution of slower development when tested in the ancestral medium.

Developmental rate and larval density dependence

There was no significant relationship between change in developmental rate on soy and change in larval density dependence ($t_{29} = -0.787$, $p = 0.438$). Moreover, there was no significant correlation between change in developmental rate on wheat and change in larval density dependence ($t_{29} = -1.750$, $p = 0.091$).

Offspring count analysis

The 95% confidence set of models included the model with main effects of hybridization, environment, and time (ΔAIC = 5.558, w = 0.057; Table III-3) and the model with just main effects of environment and time (ΔAIC = 0.00, w = 0.915; Table III-3). Parameter estimates for the fixed effects were very similar, so we only report those of the best model (Table III-5). Productivity (the number of offspring surviving to day 28) was the same for hybrid and parental populations, decreased slightly over time, and was consistently greater in wheat medium (Table III-5).

Testing for trade-offs

We found no evidence of an initial or final trade-off for productivity or developmental rate. On the contrary, there was a positive relationship between wheat and soy productivity at week 12 ($t_{157} = 3.47$, $p < 0.001$) and week 44 ($t_{157} = 2.93$, $p = 0.004$).

Discussion

The results of our developmental stage analysis clearly show hybrid lines evolved increased developmental rates on soy flour much more rapidly than non-recombinant lines. Although hybridization increased the rate of evolution of development, hybridization did not affect productivity (a combination of fecundity and larval survival). While we found no evidence of a trade-off for productivity or developmental rate, hybrid lines experienced a less severe decrease

in developmental rate in the ancestral environment than non-recombinant lines. Larval developmental rate was positively correlated with change in adult density experienced by the mother, possibly as a consequence of stress in crowded populations. Overall, our results support the idea that hybridization consistently promotes transgressive evolution in novel environments, manifested at both individual and population levels.

Hybridization increased rate of adaptation to soy

While soy flour significantly hindered development for all beetles initially, hybrid lines quickly surpassed non-recombinant lines in developmental rate in soy flour (Figure III-1). This was probably not due to simple hybrid vigor as initial developmental rates were estimated to be very similar. Initially, both hybrid and non-recombinant lines produced mostly larvae (57%) and pupae (38%) after 28 days of development in soy flour while producing almost exclusively adults (96%) in wheat. After 44 weeks of selection on soy, non-recombinant developmental rates in soy changed little (Figure III-1), while hybrid lines produced relatively more adults (12%) and pupae (53%) and fewer larvae (35%).

Our previous research demonstrated hybridization increased rates of adaptation to soy flour through the evolution of milder density dependent effects of larvae on recruitment (see Chapter 2). However, changes in developmental rate on soy are independent of adaptive changes in density dependent larval demographic traits. This would suggest that our experimental populations have evolved not just one, but rather a suite of adaptations to soy in just 44 weeks (11 generations), facilitated by hybridization. That is, hybridization can open multiple pathways for transgressive evolution.

Decrease in productivity

Despite the significant population growth observed in most experimental populations (see Chapter 2), individual productivity decreased over the course of the experiment. Productivity confounds fecundity, embryo and larval mortality, and the effects of cannibalism and crowding, but given generally increasing population sizes and evolution of milder larval density dependent effects it seems counterintuitive for assayed productivity to decrease over time. It is possible that the small assay vials increased larval density relative to population containers to such a degree that larval cannibalism increased facultatively. Alternatively, negative larval interactions might be mitigated by the presence of adults and/or additional eggs, both of which were absent from the assay vials.

Decrease in developmental rate on wheat

We did not detect any trade-offs between developmental rate in soy and wheat, but both hybrid and non-recombinant lines evolved decreased developmental rates on wheat medium (Figure III-1). That is, all populations lost performance in the ancestral environment (wheat medium), but

the magnitude of this loss was not associated with the magnitude of performance gains in the novel environment (soy medium). The trend of decreasing developmental rate in wheat is most likely caused by genetic drift of traits that experienced relaxed selection in soy flour and population bottlenecks during weeks 16 and 20 (see Chapter 2). This result suggests that the genes underlying changed developmental rate in soy are not associated with those underlying changed developmental rate in wheat.

Trans-generational effects of population growth

Although a serendipitous discovery, we report that demographic conditions in the adult population can produce a trans-generational effect on developmental rate. Females taken out of growing populations produced faster developing offspring than females taken out of declining populations. Trans-generational environmental effects are not uncommon in insects and can influence population dynamics and produce false signals of adaptation (Peters and Barbosa 1977; Rossiter 1991; Fox et al. 1997; Morag et al. 2011). However, including this environmentally-based maternal effect in our developmental rate model improved the signal of change in developmental rate, so it is unlikely that our inferences regarding developmental rate adaptation are spurious. A trans-generational effect of maternal population density on larval developmental rate has been reported in parasitoid wasps (Morag et al. 2011). However, to our knowledge, this is the first instance of adult population *growth rate* producing an environmentally-based maternal effect on larval development. The implication is that there are time-lagged feedbacks between population demographic rates and individual developmental rates. This environmentally-based maternal effects could help explain fluctuating population dynamics (Chitty 1960; Boonstra and Krebs 1979; Boonstra and Boag 1987; but see: Benton et al. 2001; Plaistow et al. 2006; Plaistow and Benton 2009). How these environmental/phenotypic dynamics interact with natural selection in evolving populations is largely unknown. However, we found evidence of both an environmentally-based maternal effect and genetic change in larval development.

Conclusions

We show that hybrid lines have responded rapidly to dietary selection for increased developmental time. In contrast, non-recombinant lines seem to be limited by standing genetic variation in developmental rate. *T. castaneum* can rapidly evolve increased developmental rates in response a harsh novel medium (Bergerson and Wool 1988; Agashe et al. 2011). However, in contrast to the results of Agashe et al. (2011), we found that the increased genetic variation from hybridization promoted adaptation to a novel medium via the evolution of accelerated developmental rate. Additionally, larval development appears to be modified by the population dynamics experienced by their parents, which raises additional questions about the interactions between population dynamics and evolutionary outcomes.

Although we did not detect any initial or evolved trade-offs, we report depression of developmental rate in the ancestral environment after selection in a novel environment, most likely due to genetic drift. This by-product decline in performance could still be important for adaptive diversification, even though it is not a true trade-off. Hypothetically, the offspring of soy-adapted lines that migrated to populations maintained in wheat would be at a selective and competitive disadvantage in wheat. This would limit gene flow and could lead to reproductive isolation (Schluter 2000; Coyne and Orr 2004).

Our research has demonstrated that hybridization can accelerate ecological transitions from one environment to another. Many ecological invasions are associated with hybridization (reviewed in: Ellstrand and Schierenbeck 2000; but see: Benvenuto et al. 2012), but experimental support for a causal relationship is lacking. If our result is generalizable, it could mean that hybridization potential should be considered as an important risk factor for evaluating a species' invasiveness. Moreover, many conservation projects grapple with the population genetic and evolutionary consequences of hybridization for endangered populations (Moritz 1999; Wolf et al. 2001; Fitzpatrick and Shaffer 2007; Fitzpatrick et al. 2010). Based on our results, it is possible that hybridization could help endangered species adapt to changing landscapes, resources, and climate.

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Appendix III. Figures and Tables

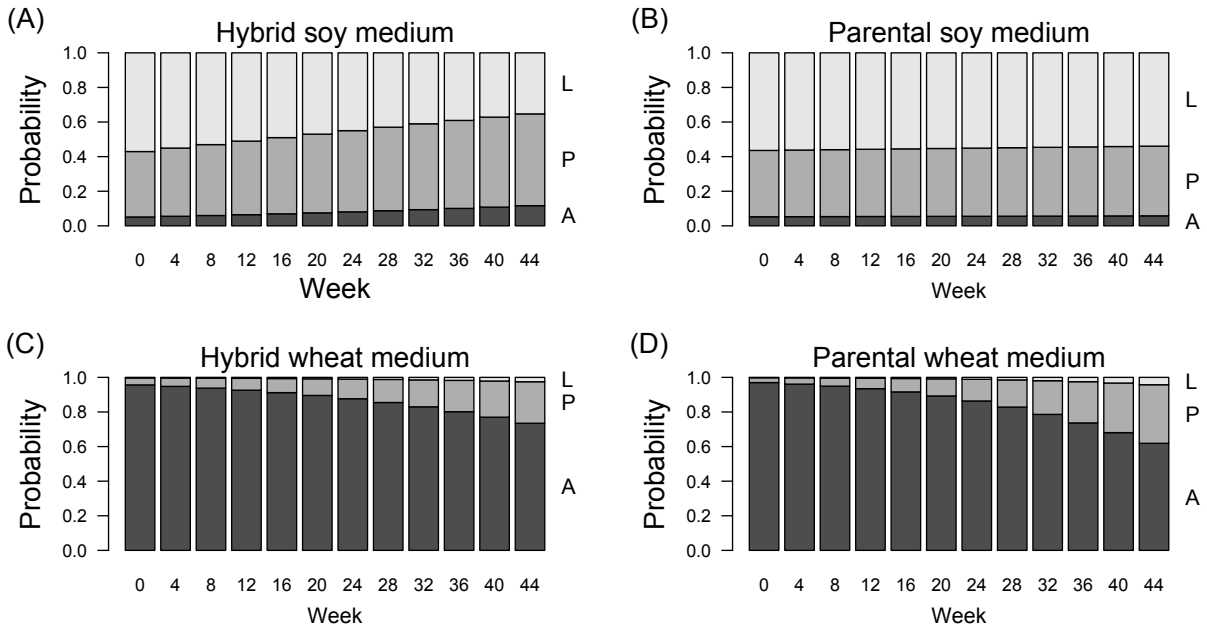

Figure III-1. Change in the age class distributions of beetles from (A) hybrid lines reared on soy medium, (B) parental lines reared on soy medium, (C) hybrid lines reared on wheat medium, and (D) parental lines reared on wheat medium. Bars represent the fitted marginal probabilities of developmental transition to larva (light grey, "L"), pupa (medium grey, "P"), and adult (dark grey, "A") age classes after 28 days incubation.

Table III-1. Developmental rate analysis model selection, stage 1. Models included in the 95% confidence set are in bold.

Model	Fixed effects[1]	DF	AIC	**Δ**AIC	w^2
m0	Hybrid*Time*Medium	12	12319.38	15.695	0.000
m1	Hybrid*Time*Medium+log(Tot)	13	12318.54	14.854	0.001
m2	Hybrid*Time*Medium+log(Tot_l)	13	12321.12	17.430	0.000
m3	Hybrid*Time*Medium+**Δ**Tot	13	12317.46	13.767	0.001
m4	Hybrid*Time*Medium+log(A)	13	12321.35	17.663	0.000
m5	Hybrid*Time*Medium+log(A_l)	13	12310.13	6.438	0.038
m6	**Hybrid*Time*Medium+ΔA**	**13**	**12303.69**	**0.000**	**0.951**
m7	Hybrid*Time*Medium+log(L)	13	12315.87	12.180	0.002
m8	Hybrid*Time*Medium+log(L_l)	13	12313.71	10.020	0.006
m9	Hybrid*Time*Medium+**Δ**L	13	12321.24	17.549	0.000

[1]An asterisk indicates interactions between terms and all lower order interactions and main effects. A, L and Tot refer to the number of adults, larvae, and sum of both censused at the time the female was removed for the larval development assay. The subscript "lag" refers to the number of adults, larvae, or sum of both from the previous census. The Δ refers to the log change in number of adults, larvae, or sum of both from the previous census to the current census. All models also included random intercepts for maternal line, paternal line, and replicate population.
[2]Model weight, *w*, is equivalent to a Bayesian posterior probability dependent on the model set.

Table III-2. Developmental rate analysis model selection, stage 2. Models included in the 95% confidence set are in bold.

Model	Fixed effects[1]	DF	AIC	ΔAIC	w^2
nf	none	5	19324.79	7022.322	0.000
m0	ΔA	6	19326.28	7023.814	0.000
m1	**Hybrid*Time*Medium+ΔA**	**13**	**12303.69**	**1.222**	**0.341**
m2	**Hybrid*Time+Hybrid*Medium+Time*Medium+ΔA**	**12**	**12302.47**	**0.000**	**0.628**
m3	Hybrid*Medium+Time*Medium+ΔA	11	12309.12	6.653	0.023
m4	Hybrid*Medium+Time*Hybrid+ΔA	11	12472.19	169.724	0.000
m5	Hybrid+Time*Medium+ΔA	10	12311.31	8.842	0.008
m6	Time*Medium+ΔA	9	12317.28	14.811	0.000
m7	Medium+Time*Hybrid+ΔA	10	12472.68	170.215	0.000
m8	Time*Hybrid+ΔA	9	19271.98	6969.511	0.000
m9	Medium+Time+Hybrid+ΔA	9	12481.66	179.189	0.000
m10	Medium+Time+ΔA	8	12487	184.534	0.000

[1] An asterisk indicates interactions between terms and all lower order interactions and main effects. ΔA refers to the log change in number of adults from the previous census to the current census. All models also included random intercepts for maternal line, paternal line, and replicate population.
[2]Model weight, *w*, is equivalent to a Bayesian posterior probability dependent on the model set.

Table III-3. Productivity analysis model selection. Models included in the 95% confidence set are in bold.

Model	Fixed effects[1]	DF	AIC	ΔAIC	w^2
nf	none	5	4466.27	236.941	0.000
m0	ΔA	6	4455.58	226.249	0.000
m1	Hybrid*Time*Medium+ΔA	13	4257.57	28.244	0.000
m2	Hybrid*Time+Hybrid*Medium+Time*Medium+ΔA	12	4250.38	21.053	0.000
m3	Hybrid*Medium+Time*Medium+ΔA	11	4242.96	13.629	0.001
m4	Hybrid*Medium+Time*Hybrid+ΔA	11	4243.29	13.959	0.001
m5	Hybrid+Time*Medium+ΔA	10	4242.20	12.874	0.001
m6	Time*Medium+ΔA	9	4236.65	7.317	0.024
m7	Medium+Time*Hybrid+ΔA	10	4242.33	12.997	0.001
m8	Time*Hybrid+ΔA	9	4454.60	225.268	0.000
m9	**Medium+Time+Hybrid+ΔA**	**9**	**4234.89**	**5.558**	**0.057**
m10	**Medium+Time+ΔA**	**8**	**4229.33**	**0.000**	**0.915**

[1]An asterisk indicates interactions between terms and all lower order interactions and main effects. ΔA refers to the log change in number of adults from the previous census to the current census. All models also included random intercepts for maternal line, paternal line, and replicate population.
[2]Model weight, *w*, is equivalent to a Bayesian posterior probability dependent on the model set.

Table III-4. Parameter estimates for developmental rate analysis. Model-averaged estimates with unconditional standard errors of the change in the odds of a developmental transition after 28 days incubation for each parameter. A colon indicates an interaction between parameters.

Parameter	Estimate	SE	z	
Parental	0.014	0.254	0.054	
Time	0.081	0.016	4.960	*
Wheat	6.000	0.165	36.389	*
ΔA	0.174	0.041	4.198	*
Parental:Time	-0.070	0.032	-2.155	*
Parental:Wheat	0.389	0.284	1.369	
Time:Wheat	-0.268	0.022	-12.082	*
Parental:Time:Wheat	-0.045	0.051	-0.881	

*Indicates significance based on approximate z scores ($\alpha = 0.05$).

Table III-5. Parameter estimates for productivity analysis. Estimates with standard errors of the change in productivity (total number of offspring surviving 28 days of incubation) for each parameter.

Parameter	Estimate	SE	DF	t	p
Intercept	1.273	0.059	1789	21.729	< 0.0001
Wheat	0.463	0.030	1789	15.268	< 0.0001
Time	-0.033	0.006	1789	-5.295	< 0.0001
ΔA	0.144	0.024	1789	6.027	< 0.0001

Conclusion

Chapter 1

Bateson's model of hybridogenic hopeful monsters and the Dobzhansky-Muller incompatibility model of hybrid inviability are both cases of transgressive segregation. The Bateson, Dobzhansky-Muller, and complementarity models are special cases of the general quantitative genetic model, thus reconciling sudden and gradual origins of novelty without requiring a special class of mutations or population dynamics.

Transgressive segregation might be an important mechanism promoting sudden phenotypic changes and ecological transitions in evolution. Even if most of the variation produced is deleterious, a rare transgressive hybrid genotype could rapidly fix in a population or establish a novel lineage. Admixture can simultaneously bring together many new combinations of alleles, generating multilocus novelties that might never have appeared via gradual accumulation of new mutations in a single population. Gene exchange is not the sole, nor even necessarily most likely, source of evolutionary novelty (Meyer 2002; Moczek 2008), but is perhaps the most likely mechanism of sudden, population level change.

Chapter 2

In our experiment, adaptation predominantly took the form of reduced density dependence. Evolutionary change in population regulation facilitated successful ecological transition to the novel habitat. The observed evolutionary changes affecting population dynamics occurred on approximately the same timescale as population dynamics, making the interplay of ecological and evolutionary dynamics an exciting aspect of this system. Our results demonstrate that hybridization can be a crucial factor affecting the speed and magnitude of evolutionary change, and therefore the tempo and outcome of eco-evo dynamics.

We provide evidence in this article of rapid adaptation to a harsh novel environment and population growth being facilitated by hybridization. Transgressive evolution during hybridization has the potential to elicit rapid population growth and adaptation to a novel environment. These results support the generality of the "Evolutionary Novelty" model of hybridization (Arnold 1997) and the importance of hybridization in the interplay between ecology and evolution in nature.

Chapter 3

We show that hybrid lines have responded rapidly to dietary selection for increased developmental time. In contrast, non-recombinant lines seem to be limited by standing genetic variation in developmental rate. Additionally, larval development appears to be modified by the population dynamics experienced by their parents, which raises additional questions about the interactions between population dynamics and evolutionary outcomes.

Although we did not detect any initial or evolved trade-offs, we report depression of developmental rate in the ancestral environment after selection in a novel environment, most likely due to genetic drift. This by-product "trade-off" could still be important for adaptive diversification. Hypothetically, the offspring of soy-adapted lines that migrated to populations maintained in wheat would be at a selective and competitive disadvantage in wheat. This would limit gene flow and could lead to reproductive isolation (Schluter 2000; Coyne and Orr 2004).

Our research has demonstrated that hybridization can accelerate ecological transitions. Many ecological invasions are associated with hybridization (reviewed in: Ellstrand and Schierenbeck 2000; but see: Benvenuto et al. 2012). If our result is generalizable, it could mean that hybridization potential should be considered as an important risk factor for evaluating a species' invasiveness. Moreover, many conservation projects grapple with the population genetic and evolutionary consequences of hybridization for endangered populations (Moritz 1999; Wolf et al. 2001; Fitzpatrick and Shaffer 2007; Fitzpatrick et al. 2010). Based on our results, it is possible that hybridization could help endangered species adapt to changing landscapes, resources, and climate.

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Vita

Dylan Robert Dittrich-Reed was born in Memphis, Tennessee in 1983, but raised in Napa, California. He attended Napa Valley High School and graduated in 2001. Dylan was active in the Boy Scouts of America and achieved the rank of Eagle Scout. He attended the University of California, Davis where he earned a BS in Evolution and Ecology in 2005. Dylan met his wife, Megan, during UCD summer advising in 2001 and they married after graduation in 2005. From 2005 to 2007 Dylan worked as a laboratory technician for H. Bradley Shaffer at UCD where he worked on projects involving conservation of the endemic tiger salamander (*Ambystoma californiense*). Studying hybridization between A. californiense and the invasive barred tiger salamander (*A. mavortium*) sparked Dylan's interest in the evolutionary consequences of hybridization.

Dylan enrolled in the graduate program at the University of Tennessee, Knoxville in 2007 to study under Benjamin M. Fitzpatrick. Initially, he was interested in studying a putative case of natural hybridization between two species of dusky salamander (*Desmognathus quadramaculatus* and *D. marmoratus*). It took him three years to realize that some vertebrates are not very good lab animals. The focus of his dissertation work shifted to an empirical test of the creative potential of hybridization using red flour beetles (*Tribolium castaneum*) as a model. Dylan received generous funding from the National Science Foundation to expand his research to study changes in the bacterial communities of the beetles during hybridization. During his tenure at UTK, Dylan also studied pedagogy and hopes to be an excellent teacher as well as scientist.

Dylan and Megan produced the two most beautiful, sweet, and gifted children during his tenure at the University of Tennessee: Rylan (born 2008) and Pippa (born 2011).